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GROWTH OF MAIZE SEEDLINGS IN RELATION TO TEMPERATURE

PHILIP AUGUSTUS LEHENBAUER

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Thesis submitted in partial fulfilment of the requirements for the Degree of Doctor of Philosophy in Botany in the Graduate School of the University of Illinois, 1914

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By

PHILIP AUGUSTUS LEHENBAUER

A.B. Westminster College, 1907; A.M. Millikin University, 1909

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GROWTH OF MAIZE SEEDLINGS IN RELATION TO TEMPERATURE

PHILIP AUGUSTUS LEHENBAUER

ABSTRACT[1]

From the work of former investigators it has appeared that the curve of plant growth in relation to temperature is quite irregular, exhibiting not one principal apex only but, in some instances at least, a double optimum. Whether this apparent double optimum is to be regarded as the result of the interaction of other, uncontrolled, external factors influencing growth, or whether it may be due to internal causes has not been determined.

The published data concerning optimum temperatures for plant growth vary rather widely as to the temperatures indicated as optima. This may be due to the fact that an important factor, that of time, has usually been disregarded in experimentation along this line. Recent researches on optimum temperatures for other physiological activities have shown clearly that a consideration of the time factor is of the utmost importance in such studies. It is thus suggested that the discrepancies of earlier investigations upon temperature optima for growth may be due to the determination of the growth increments at too long intervals. It is also possible that a study involving a wider range of temperatures than has usually been employed, may throw light upon the general problem.

In the experiments here discussed an attempt has been made to keep all the conditions for growth considerably more uniform than has usually been the case with earlier investigations of this sort. Maize seedlings were used, grown practically in darkness and with approximately constant temperature. The relative humidity of the air was always very close to 95 per cent. Due attention was also given to the time factor in its relation to the rates of growth at the different temperatures. Measurements of the growth increments of the shoots were hourly in most cases, and observation was continued for periods ranging in length from 12 to 39 hours. The main results and conclusions brought out by a study of the detailed data presented in the tables, are summarized below.

1. The somewhat widely accepted idea that the curve of growth in relation to temperature shows two optima is not at all substantiated in this work with the shoots of maize seedlings grown in water culture, practically in darkness, and with relative air humidity of 95 per cent.

[1] The manuscript of this paper was received August 1, 1914. This abstract was preprinted, without change from these types and was issued as Physiological Researches Preliminary Abstracts, vol. 1, no. 5, November 1914.

2. The optimum temperature for growth of shoots of maize seedlings in water culture, *for a 12-hour period,* is shown to be 32°C.

3. The optimum temperature for growth, under these conditions, is found to change as the length of the period of exposure is altered.

4. At high temperatures (31°C. and above), for shoots of maize seedlings under these experimental conditions the initial growth-rate is not maintained, there being a marked falling off in this rate during prolonged periods of exposure.

5. This decrease in the growth rate with prolonged periods at high temperatures makes it necessary to consider the length of the periods for which average growth rates are obtained, in defining the optimum for growth of these shoots. Indeed, it appears that the term *optimum temperature* for growth, in this case at least, is *quite without meaning unless the length of the period of exposure is definitely stated.*

6. The fall in growth rate here brought out is similar to the decrease in rate of certain other physiological processes under the influence of high temperatures during prolonged periods.

7. At temperatures near the minimum (12–14°C.) for the growth of shoots of maize seedlings under the conditions here employed, no decrease in the growth rate is shown, even with rather prolonged periods of exposure.

8. The growth rate at medium temperatures accords with the van't Hoff law, showing a doubling of the rate for each rise of 9° or 10°C.

INTRODUCTION

Rising temperature has long been known to be attended by increased rate of enlargement in growing plants, unless the initial temperature be too high or the temperature change be excessive. It is also generally recognized that the growth curve in relation to temperature, shows three cardinal points: (1) the minimum, a temperature below which no growth is exhibited, (2) the optimum, at which growth is greatest, and (3) the maximum, at which growth again comes to a standstill.

Considerable discussion has recently appeared concerning the true position and the meaning of the optimum temperature for plant growth. Earlier investigators,[2] in their studies regarding the effects of temperature on growth, subjected the plant to a given temperature for a longer or shorter period of time, and measured the increment of growth for that period. The temperature at which the highest growth rate occurred, within the time period chosen, was considered as the optimum temperature for growth. A study of the published data bearing upon the optimum temperature for growth

[2] Sachs, J., Textbopk of botany, translated by A. W. Bennett, assisted by W. T. Thistleton-Dyer. Oxford 1875.

DeVries, H., Matériaux pour la connaissance de l'influence de la température sur les plantes. Arch. Néerland. 5: 385–401. 1870.

Koeppen, W., Wärme und Pflanzenwachsthum. Bull. Soc. Imp. Nat. Moscou 43II: 41–110. 1870.

reveals a wide range of variation in its position on the thermometer scale. Sachs [75] placed it at 34°C. for seedlings of flowering plants, and at 33.7°C. for shoots of seedlings of *Zea mais*. Koeppen [70] gives two optima for the shoot of maize, 30° and 33.5°C.; and Sachs [75] states that De Candolle placed it, for the same seedling, at 28°C. Davenport,[3] using Koeppen's data, placed the optimum at 32.4°C.

The most thorough study of the relation of temperature to growth in plants, thus far reported, is that of Koeppen. Working with a number of different seedlings, this author obtained growth curves, in relation to temperature, that are markedly irregular. In many instances these curves show double optima. For maize, Koeppen's curve shows the two optima to lie at 30° and 33.5°C., as above indicated, with a decided drop in the curve, corresponding to intervening temperatures. This curve is here reproduced as figure 1.

The fact that the optimum for growth of the seedling of *Zea mais* as well as for other seedlings, has been placed by different workers at such different temperatures makes further study of this problem desirable. The methods heretofore used in this study have been essentially the same and the accuracy of the observations themselves is not to be questioned; in seeking an explanation for such wide discrepancies as have been noted for maize seedlings we must consequently endeavor to find some condition or conditions not adequately considered by the earlier writers, which may be responsible for the differences in question.

Of course the uncontrolled or neglected conditions which have made for discrepancies in the position of the optimum temperature for growth, as this has been determined, may be supposed to have been related to differences in the physiological nature of the plants employed. For example, different varieties of maize may exhibit different temperature optima because of internal conditions not yet amenable to experimentation; seed of the same variety but produced in different localities or in different years, may furnish seedlings of widely different physiological properties; and, finally, seeds with the same internal properties may give rise to very different seedlings, if germination occurs under sufficiently different environmental conditions. With these suggested possibilities experimentation cannot at present deal and attention is to be first confined to a study of the external, controllable, conditions that may possibly influence the position of the apparent optimum in question.

Clausen's[4] work on the relation of temperature to respiration, that of Chudiakow[5] on fermentation and that of Matthaei[6] on photosynthesis, sug-

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[3] Davenport, C. B., Experimental morphology. New York, 1908.

[4] Clausen, H., Beiträge zur Kenntnis der Athmung der Gewächse und des pflanzlichen Stoffwechsels. Landw. Jahrb. **19**: 893–930. 1890.

[5] Chudiakow, N., Untersuchungen über die alkoholische Gährung. Landw. Jahrb. **23**: 391–532. 1894.

[6] Matthaei, Gabrielle L. C., Experimental researches on vegetable assimilation and respiration. Phil. Trans. Roy. Soc., London (B)**197**: 47–105. 1904.

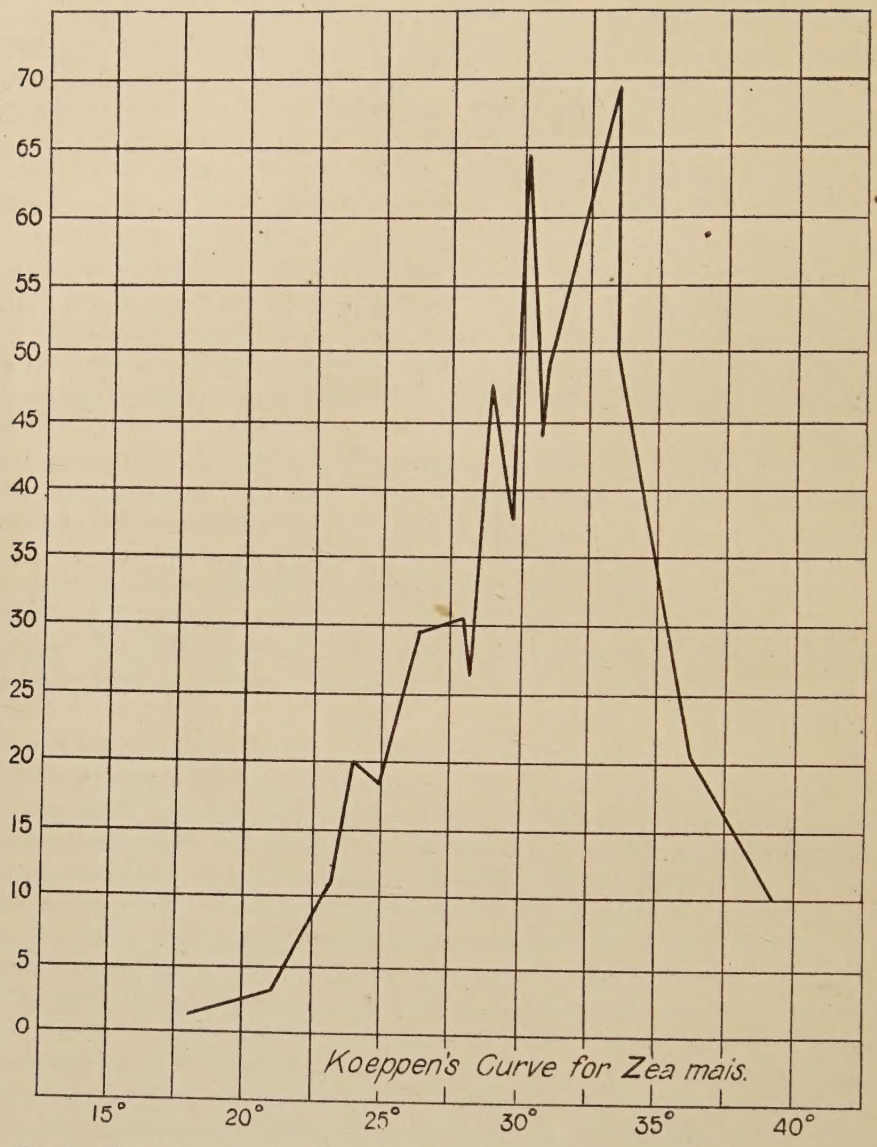

FIG. 1. Graph showing the relation of temperature to growth rate in shoots of maize seedlings, as recorded by Koeppen. The so-called double maximum, with the pronounced depression between the two apices, is shown, together with other irregularities.

gest that the time factor, so important in the consideration of the optimum temperature for the physiological processes just mentioned, may possibly, and even probably, play an equally important rôle in the determination of

the apparent optimum temperature for growth. In the important contributions of F. F. Blackman[7] and of Jost,[8] it has been clearly pointed out that this time factor is of fundamental importance in the consideration of the cardinal points of physiological activities in general. In the process of photosynthesis, for example, the initial rate is not long maintained at high temperatures; after a short time, at such temperatures, the rate decreases with more or less rapidity. The same principle holds true for other physiological processes, as respiration, fermentation, etc. Owing to this decrease in the initial rate of physiological action at high temperatures, the position of the optimum shifts with the temperature and with the length of the period of exposure, which is the time elapsing between the application of the given temperature and the first measurement of increment thereafter. Thus, the position of the optimum for such a process as respiration or photosynthesis is found to occur at a higher temperature by an observer who takes his first reading after *one* hour than by another who takes his first reading after *three* hours. In the recorded work on the relation between plant growth and temperature the data were secured from a single measurement in each case, this measurement being obtained usually after the plant had been exposed to the given temperature for a period of 48 hours. Some investigators have measured the increments of growth at much shorter time intervals, but even in such cases a wide range of temperatures has not been employed. Askenasy,[9] in his experiments on the growth of roots of maize, did not go beyond a temperature range of from 28° to 29°C. Godlewski[10] worked only with medium temperatures. True[11] did not carry his experiments beyond a temperature of 30°C., the apparent optimum in his study.

On the whole, it is clear that no very thorough knowledge of temperature optima for plant growth can be attained without much more elaborate study than has yet been carried out, and the considerations just set forth seemed to furnish a new point of view and a promising mode of attack. The present study was undertaken, at the suggestion of Prof. C. F. Hottes, of the University of Illinois, as an investigation of the relations holding between constant temperatures, lengths of exposure periods, and growth rates.

Seedlings of *Zea mais* were chosen for the work, the roots being in nutrient solution and the shoots in circulating air with 95 per cent. of relative humidity, the whole in very weak diffuse light. The experimentation was carried out in the Botanical Laboratory of the University of Illinois. It is with pleas-

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[7] Blackman, F. F., Optima and limiting factors. Ann. Bot. **19**: 281–95. 1905.

[8] Jost, Ludwig, Ueber die Reaktionsgeschwindigkeit im Organismus. Biol. Centralbl. **26**: 225–43. 1906.

[9] Askenasy, E., Ueber einige Beziehungen zwischen Wachsthum und Temperatur. Ber. Deutsch. Bot. Ges. **8**: 61–94. 1890.

[10] Godlewski, E., Ueber die Beeinflussung des Wachsthums der Pflanzen durch äussere Factoren. Bull. Internat. Acad. Sci. Cracovie **1890**[I]: 166–76. 1890. Abstracted in Bot. Centralbl. **47**: 307–9. 1891.

[11] True, R. H., On the influence of sudden changes of turgor and of temperature on growth. Ann. Bot. **9**: 365–402. 1895.

ure that I acknowledge my indebtedness to Professor Hottes for suggesting the problem, and for valuable and helpful criticisms, especially in the construction of the apparatus. It is also a pleasure for me to acknowledge many helpful suggestions, as to the presentation of the results, received from Prof. B. E. Livingston, of the Johns Hopkins University.

APPARATUS

General. The main apparatus requirements for experimentation such as that here undertaken are the following: the plant chambers must be supplied with air free from laboratory gases; the air humidity must be capable of accurate adjustment and maintenance; it must be possible to maintain constant temperature in the chambers, for relatively long periods of time, and the temperature must be readily and conveniently capable of change when this is desired; and, finally, measurements of the growth increments of the plants must be made with adequate precision and without disturbing the plants or otherwise altering the conditions controlling their growth. The apparatus here employed, designed to secure these features, consisted essentially of (1) the thermostats, (2) the arrangement for constant air humidity, and (3) the plant chambers. These parts will now be briefly described.

The thermostats. A tank of water (approximately 105 cm. long, 75 cm. wide and 30 cm. high) contained submerged Winkler glass coils, through which air was passed to the plant chambers, thus becoming warmed. The same tank contained the saturation chamber, where the air was brought to the proper humidity. Three other thermostat tanks (about 33 cm. long, 20 cm. wide and 33 cm. high, the two square sides of glass) each contained a plant chamber surrounded by water. The glass sides were covered with light-proof curtains (of leatheret, such as is used for carriage covers), excepting while measurements of the plants were being made. These four thermostat tanks were all supplied with electric heating coils, so arranged that the water of the tank was constantly and adequately circulated through them by means of rotating stirrers. An ordinary thermometer suspended in the water showed the temperature, which was controlled in each case by automatic thermo-regulators.[12] The last-named instruments were enclosed in submerged water-tight chambers provided with lead tubes for the electric connections. "Eastman" 4 by 5-inch plate-developing tanks, on the market for use in photography, were found very suitable for these chambers; the lids may be readily removed for adjusting the regulators, and the closure is absolutely water tight.

With this arrangement no difficulty was experienced in maintaining the temperature of the plant chambers constant within a range of fluctuation of

[12] These were of a type much like that described by Land (Land, W. J. G., An electrical constant temperature apparatus. Bot. Gaz. **52**: 391–9. 1911), with a tongue of steel and hard rubber swinging to and fro with changes of temperature. They were constructed by Mr. G. R. Smith, Electrician of the University of Illinois.

0.5°C. The fluctuation always lay above the temperature given. Thus, in the case of an experiment at 20°, the actual variation of the chamber temperature was from 20° to 20.5°C.

The arrangement for constant air humidity. Air drawn from out-of-doors was first dried by passing through drying chambers with calcium chloride and sulphuric acid. It was next recharged with water vapor to a definite degree by passing through the saturation chamber mentioned above as submerged in the large thermostat tank, this chamber being provided with an 8 per cent. solution of sodium chloride, the proper concentration[13] to give the required air moisture (95 per cent. relative humidity). The main saturation chamber was a glass bottle of about 11 liters capacity, about two-thirds filled with the solution, through which the air was made to bubble.

After being properly charged with moisture in the main saturation chamber the air was conducted through lead tubes to each of the three small thermostat tanks, in each of which it passed through another, smaller, saturation chamber before entering the corresponding plant chamber. These latter saturation chambers served to renew any moisture lost from the air in transit through the tubes, which were unavoidably somewhat cooler than the thermostat tanks; in the small tanks the air was thus rewarmed and recharged with water vapor, to the requisite temperature and humidity. From the plant chambers the air was withdrawn, by means of one or two water aspirators (arranged to be used singly or combined), and was discharged outside of the apparatus. The aspiration tube was joined to each of the three plant chambers, and the rate of air movement through these was regulated by means of mercury manometers connected with the chambers, and a series of stop-cocks in the supply tubes.

The plant chambers. The plant chambers were constructed of glass jars 24 cm. high by 12 cm. square, with a short cylindrical neck above, the diameter of the neck being but little less than that of the prismatic basal portion. The glass neck was prolonged upward (15 cm.) by a cylinder of tinned sheet iron, attached by plaster of Paris, the free surface of the latter being covered with a hard cement of rubber-resin mixture. The metal portion of the chamber was covered inside and out with black acid-proof, non-fuming paint ("Probus" brand, made by Wolff and Dolan, San Francisco, Calif.) Two nipples near the upper edge provided passage for the two air tubes. Of these latter, the exit tube reached nearly to the bottom of the chamber, the other (air inlet) merely through the wall. A friction lid closed the main

[13] If H denotes percentage of relative humidity, then $H = 1 - na$, wherein n is the weight of solute in 100 g. of water, and a is a constant varying with the nature of the salt employed. This constant, a, is 0.00601 for sodium chloride. (See Davenport [08], page 351. Also see:—Lesage, P. Recherches expérimentales sur la germination des spores du Penicillium glaucum. Ann. Sci. Nat. Bot. VIII. **1**: 309–22. 1895. Lesage derives the value of a from work of Wüllner:—Wüllner, A, Versuche über die Spannkraft des Wasserdampfes aus wässerigen Salzlösungen. Ann. Phys. und Chem. **103**: 529–62. 1858. **105**: 85–117. 1858). According to this formula, a solution of sodium chloride containing 8 g. of salt to 100 g. of water should give 95 per cent. of relative humidity in air with which the solution is in equilibrium: $H = 1 - 8 \times 0.00601 = 0.95$.

opening at the upper end of the metal cylinder, the joint being further sealed and rendered air-tight with a mixture of modelling clay and petrolatum (vaseline), such as is recommended by Crocker.[14] This lid could be readily removed and replaced, thus furnishing ready access to the chamber, for inserting and removing the culture bottles.

The plant chambers were immersed in the water of the thermostats, the metal neck remaining above the water level. When equipped for an experiment each chamber contained a thermometer and Lambrecht polymeter, besides the culture bottle and its two plants. Readings of the temperature and relative humidity of the chambers were made hourly and recorded with the hourly increments of growth. The Lambrecht polymeter (hair hygrometer) in each plant chamber indicated that the relative air humidity fluctuated not more than 1.5 per cent. of relative humidity in either direction, while the apparatus was in operation. The actual humidity as indicated by the Lambrecht instruments, varied from a minimum of 93 to a maximum of 96 per cent., making it safe to consider it as approximately 95 per cent.

Such slight changes in temperature and humidity conditions as were observed exhibited no relation to the growth fluctuations, showing that the constancy of temperature and humidity control was adequate for the work in hand.

METHODS

Manipulation of apparatus. In beginning an experiment the thermostats and the plant chambers were first brought to the temperature desired. Sufficient time was allowed for the glass walls of the plant chambers to attain the temperature of the water of the thermostats. When low temperatures were employed the water in the thermostats was first cooled by adding ice, the thermo-regulators maintaining the somewhat higher temperature desired. On cold days it was found advantageous to open the windows and thus to cool the room below the temperature required for the thermostat.

After the desired temperature had been attained within the plant chambers, the plants, polymeter and thermometer were put in place and the top was securely closed. Then the aspirators were started and adjustment made until a constant and uniform flow of air through each chamber was attained. An interval of 2 hours was allowed to elapse for the culture bottle and its solution, the plants, the polymeter and the thermometer to attain the temperature of the chamber, and for the plants to accommodate themselves to the new conditions. After this interval measurements of the growth increments of the shoots were started and continued, at intervals, throughout the experiment.

[14] Knight, L. I., and Crocker, W., Toxicity of smoke. Bot. Gaz. 55: 337–71. 1913. Page 339.

The plants were practically in darkness during the period of experimentation; only very weak diffuse day-light, which might penetrate far into the room, and then through the water of the thermostat and the glass walls of the plant chamber, reached them by day. Light for the measurements was provided by continuously operated electric bulbs, one immediately in front of, and another behind, the thermostat, the opaque curtains being raised during each observation. The plants were never directly exposed to this light for a period longer than 40 seconds. Under these conditions the seedlings were always erect, and absolutely no day and night periodicity in growth was at any time apparent. Slight greening occurred.

The measurements were made with telescopes with cross hairs, like cathetometers. A scale graduated in half-millimeters, placed immediately behind the plant, permitted ready and sufficiently accurate measurements of the height of the tip of the shoot above the zero of this scale.

Preparation of seedlings. "Reed's Yellow Dent" maize, of the previous year's harvest, grown on the Illinois Agricultural Plots, was used. The seed was uniform and of good quality, showing a percentage of germination such as agriculturists regard as good. The grains were soaked in water for about 10 hours, and were then allowed to germinate in sphagnum moss, in a basement dark room (free from gas pipes) with a temperature of from 27° to 29°C.

When the seedlings had attained a sufficient size for experimentation (the shoots being from 10 to 12 mm. high) they were transferred on the evening preceding the day of the experiment, to wide-mouthed bottles (125 cc. capacity) of nutrient solution. These bottles were provided with 2-perforate, tightly fitting, paraffined, flat cork stoppers. The roots and seed of a seedling were passed through each perforation and each plantlet was held in place by means of the usual cotton packing above the seed. The bottles were wrapped in black paper, opaque to light. The culture bottles, each with its two seedlings, remained in the dark room during the night and the growth rates of the plants were approximately determined for this period, in order to eliminate any individuals which appeared to be abnormal. They were placed in the plant chambers on the morning of the following day. The nutrient solution employed was that known as Tollen's solution.[15] This solution is prepared in two parts, A and B. Part A consists of 2.05 g. $MgSO_4$ ($7H_2O$) dissolved in 35 cc. of water. Part B contains 4 g. $Ca(NO_3)_2$ ($4H_2O$), 1 g. KNO_3 and 1 g. KH_2PO_4, all dissolved in 35 cc. of water. The complete solution is made by combining 10 cc. of part A and 35 cc. of part B with 980 cc. of water and adding to this a few drops of an aqueous solution of ferric chloride.

The water used in the nutrient solution was first distilled, with a still having a block tin condenser. It was redistilled in hard glass. Finally it

[15] Pfeffer, W., The physiology of plants, translated by A. J. Ewart. 1: 420. Oxford, 1900.

was shaken with thoroughly washed carbon ("G. Elf" brand carbon black), as recommended by Livingston[16] and by Schreiner and Skinner,[17] to remove traces of toxic material which might be present. A fresh solution was prepared for every experiment.

POSSIBLE DISTURBING CONDITIONS

In comparing growth rates under different temperature conditions it is of course essential that all plants be similarly treated, excepting for the single condition, temperature, the influence of which is to be studied. Since any change in the environment may be expected to have some effect upon subsequent growth, at least for a limited period after the change, it became necessary to determine, by preliminary experiments, how long the disturbance of growth might be effective, which is caused by the change of bringing the seedlings under the experimental conditions. Two environmental changes which might not be without influence upon later growth, and which were unavoidable in the starting of the experiments, require attention here, the change of medium and the change of temperature. These will next be considered.

Change of medium. The transfer of the seedlings from sphagnum moss to the bottle of nutrient solution necessitated a handling and also a change of medium, which produced a decided disturbance in growth, a result which is in accord with similar observations of Askenasy [90] and of many other experimenters. An interval of 12 hours after the transfer was found amply sufficient, however, to allow the seedling to accommodate itself to the new conditions, and no effect of the transfer itself was apparent after that interval. The transfer was made as rapidly and carefully as possible, so that the shock incidental to handling was reduced to a minimum.

Change of temperature. In the experiments to be considered below, the temperature at which the growth of the seedlings was studied was often several degrees higher or lower than the temperature at which they had grown. It was thus necessary to determine the length of period required for the recovery of the plant from the temporary depression or acceleration of growth, incident to the initial change in temperature.

The effects of sudden changes of temperature on plant growth have been studied by a number of investigators. One of the first of these was Koeppen [70], who observed that an abrupt change of temperature, in either direction, brought about a lowering of the growth rate. He maintained that it is the fact of a sudden change, rather than the direction or amount of change, that affects growth.

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[16] Livingston, B. E., Further studies on the properties of unproductive soils. U. S. Dept. Agric. Bur. Soils Bull. 36. 1907.

[17] Schreiner, O., and Skinner, J. J., Ratio of phosphate, nitrate and potassium on absorption and growth [*sic*]. Bot. Gaz. **50**: 9–30. 1910.

Pedersen[18] repeated the experiments of Koeppen and obtained results which led him to a diametrically opposite conclusion. He exposed seedlings of *Vicia faba* to sudden and to gradual changes of temperature between 10° and 20°R. (12.5° and 25°C.) and reported that no evidence of any retardation of growth was manifested. He found the growth rate to depend solely on the temperature itself, the simple fact of change being without influence.

This matter was again taken up by Askenasy [90], who confined his observations to roots of maize seedlings. He found that the influence due to the fact of sudden temperature change depends upon whether the first temperature, from which the transfer is made, lies above or below the minimum temperature for growth. When the first temperature still permitted growth, change to a higher temperature was followed by an immediate resumption of the rate of growth characteristic of the higher temperature. When, however, the first temperature was near the point where growth was inhibited, change to a higher temperature was followed by a more or less tardy resumption of the normal growth rate.

The results of True [95], obtained in Pfeffer's laboratory, mainly confirm those of Askenasy. He found that the effect upon growth, of a sudden change of temperature, depends upon "the position of the lower limit." This writer concludes as follows:

> Following a sudden fall or a sudden rise of the temperature between 18°–21°C. and 0.5°–1.5°C. as extremes, the first effect seen is a slight turgor-change due to physical causes, producing, or tending to produce, a shortening in length if the temperature be lowered; or in case the temperature be raised, producing an elongation. Following this mechanical action a period of depressed growth usually follows. The duration of the depression-period depends on the position of the lower temperature limit and on the length of time of exposure to this temperature.

With higher temperatures True found that every change from 30° to 18°C. is followed by a reduction of the growth-rate during the ensuing one-fourth hour. Further effects plainly due to the change are not to be traced in the later growth. It increases or diminishes according to the internal conditions prevailing. The transfer from 18° to 30°C. is always followed by an increased amount of elongation during the ensuing fifteen minutes. As before, the growth-rate gives no further evidence of being influenced by the temperature-change. In both cases, the traceable effects of the change disappear within fifteen minutes.

The experiments of Price[19] on the influence of temperature changes as such on the rapidity of development of flower buds of fruit trees may be

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[18] Pedersen, R., Haben Temperaturschwankungen einen ungünstigen Einfluss auf das Wachsthum? Arb. Bot. Inst. Würzburg **1**: 563–83. 1874.

[19] Price, H. L., The application of meteorological data in the study of physiological constants. Ann. Report Virginia Agric. Exp. Sta. **1909–10**: 206–12. 1911.

mentioned here. Price found that "the retardation of development by cold is altogether temporary and directly proportional to the time during which the low temperature prevails." That is, there was no observable effect of temperature change as such, in his experiments.

Some tests of the influence of sudden change of temperature, amounting to five degrees, on the rate of growth of maize seedlings, were made in the present study. The temperature was first kept at 25°C. for 6 hours and was then raised, within a period of 5 minutes, to 30°C. Results of such tests are presented in table I, which is self-explanatory.

The data of table I show that the rate of growth was markedly increased during the second and third hours following the change of temperature from

TABLE I

Hourly growth increments (hundredths of a millimeter) for shoots of maize seedlings growing in practical darkness, with 95 per cent. relative air humidity, for 11 hours; the temperature being maintained at 25°C. during the first 6 hours, after which it was changed[a] and maintained at 30°C. during the remaining 5 hours.

NO. OF HOUR	NUMBER OF PLANT									AVERAGE	TEMPERATURE, C.
	1	2	3	4	5	6	7	8	9		
1	50	25	75	25	50	75	75	50	50	53	
2	25	50	75	50	50	50	75	75	50	55	
3	75	75	75	75	50	50	50	75	50	64	
4	75	75	75	75	75	75	50	50	75	69	25°
5	50	50	100	75	75	50	75	75	100	72	
6	50	75	100	75	75	75	75	75	100	78	
7	75	125	125	75	100	75	75	100	100	94	
8	100	125	175	150	150	150	150	125	150	142	
9	100	100	150	150	125	100	125	125	125	122	30°
10	100	100	125	125	100	75	100	125	100	105	
11	100	100	175	150	100	75	100	100	75	108	

[a] The temperature change occurred within a period of 5 minutes.

25° to 30°C., the rate then falling to the characteristic magnitude for the higher temperature. This result differs somewhat from those obtained by Askenasy [90] and by True [95]. As has been noted, the earlier of these two authors found no influence exerted by the fact of such a temperature change as this, *per se*. True found that such a change, from lower to higher temperature, resulted in an initial rise in the growth rate to a magnitude higher than the normal one for the higher temperature, which was very soon followed, after but 15 minutes, by a rapid fall to that normal. The essential difference between the results of True and those of the present study lies in the longer period required by my plants to assume the growth rate characteristic of the new temperature. This difference may possibly be accounted for by a difference between methods employed for changing the temperature.

With the apparatus here used the temperature of the plant chamber could be suddenly raised (in less than 5 minutes) the five degrees required, but the bottle and nutrient solution assumed the new temperature but slowly. The nutrient solution attained the higher temperature in considerable less than 2 hours, however. Whatever may have been the reason for the difference between True's results and those here recorded, it is clear from table I that the effect of temperature change itself, from lower to higher, had ceased to be appreciable, in the present study, by the end of the initial 2-hour period allowed for the plants and their surroundings to come into physical and physiological equilibrium.

Since it was intended to study the growth rate at temperatures lower as well as higher than that at which the seedlings had grown, a further series of experiments was undertaken to determine the special influence of changes from higher to lower temperature. Two lots of seedlings were grown at 20° and 29°C., respectively. A number from each lot were then placed in the plant chambers at 25°C., and the increments of growth measured. The results are shown in table II.

TABLE II

Hourly growth increments (hundredths of a millimeter) for shoots of maize seedlings growing in practical darkness, with 95 per cent. relative air humidity, for 7 hours, at a constant temperature of 25°C.; the two groups of seedlings having been previously grown with constant temperatures of 29° and 20° respectively.

NO. OF HOUR	GROUP I Seedlings grown at 29°C.					GROUP II Seedlings grown at 20°C.				
	1	2	3	4	AVERAGE	1	2	3	4	AVERAGE
1	25	25	50	25	31	75	100	100	125	100
2	50	75	75	75	69	50	75	50	100	69
3	50	50	75	75	62	75	75	50	75	69
4	50	75	75	75	69	75	75	75	75	75
5	75	50	75	100	75	75	50	75	75	69
6	75	75	100	100	87	75	75	75	75	75
7	75	100	100	75	87	100	75	75	50	75

An inspection of table II shows that the change from lower to higher temperature (20° to 25°C.) resulted in a special acceleration of growth similar to that brought out in table I, but this effect vanished in the present case after only a single hour. For the change in the other direction (from 29° to 25°C.) the data of table II show that the growth rate for the first hour following the change was lower than the final, nearly uniform rate for 26°. It thus appears that the special or "shock" influence of change from higher to lower temperature may be considered as not effective after the first hour subsequent to the change.

From the experimental data recorded in tables I and II it appears that the 2-hour period allowed to elapse in this study, between the initial tem-

perature change and the beginning of growth measurements, was amply sufficient to avoid growth rates that might have been due to the temperature change *per se*, in whichever direction the change occurred. As a further precaution in this connection, besides the 2-hour period of adjustment after the cultures were placed in the plant chamber, the culture bottle and its nutrient solution were gradually brought to the new temperature before the transfer, whenever the experiment called for a marked difference between the cultural and the experimental temperatures.

NORMAL GROWTH

In experimental work involving a large number of different individual plants the amount of variation due to unknown conditions is often very great. In the present studies there appeared considerable individual variation in the rates of growth of different plants under apparently the same environmental conditions. Occasionally a seedling exhibited a rate of growth far above or far below the general average. As is usual in such experimentation as this, such widely erratic individuals were rejected. Askenasy [90] favors such a procedure. In discussing the question here raised, he says (page 63):

> Es ist sehr wichtig, bei vergleichenden Versuchen nur mit gesunden Wurzeln zu arbeiten. Das einzige sichere Zeichen der Gesundheit einer Wurzel ist ein entsprechendes Wachsthum. Ich habe darum immer das Wachsthum der Wurzeln erst eine Zeit lang bei einer dem Optimum nahen Temperatur (26–29°) beobachtet und alle Wurzeln, die unter 1.7 mm. stündlichen Zuwache zeigten, verworfen. Pedersen bemerkt allerdings, dass "es nicht erlaubt wäre, jede langsam wachsende Wurzel als krank und abnorm zu betrachten, bloss deshalb weil sie langsam wächst." Ich bin aber anderer Ansicht. Viele Umstände, die auf das Wachsthum der Wurzeln ungünstig einwirken, sind uns nicht genügend bekannt, wir nehmen sie nur an ihren Folgen wahr, und wir werden sicherer gehen, wenn wir abnorm langsam wachsende Wurzeln verwerfen.

True [95] evidently eliminated those plants of his cultures that showed an abnormally rapid or slow growth. He states (page 368): "In the investigation only those specimens were used which, by at least an average growth, indicated a normal condition."

The seedlings used in the present studies were grown from seeds taken from selected ears of the same progeny as far as possible. Also, as far as possible, the plants of each series were from grains taken from the same ear, those from tip and butt being rejected. They were all grown under apparently identical external conditions and only those of the same age and approximately the same height were chosen for the tests. (See Pfeffer[20] in this connection.) All seedlings with shoots more than 12 and less than 10 mm. in length were rejected. Finally, before the seedlings were placed in the plant

[20] Pfeffer, W., The physiology of plants, translated by A. J. Ewart. 2: 15, 79. Oxford, 1903.

chambers, they were grown in nutrient solution for from 8 to 10 hours at a temperature of from 27° to 29°C., with measurement of the growth rate, and all whose rate deviated widely from the average of a large number were thrown out.

RESULTS

General plan of presentation. In the presentation of the numerical data, which follows, there are always two time periods involved, the period of exposure to the given temperature and the period of observation or time increment. The period of exposure is the length of time from the beginning of the growth measurements to the end of the experiment or to any chosen time before this. The periods of observation are the periods elapsing between the consecutive growth readings; thus the period of exposure is the sum of the lengths of all the periods of observation considered.

It will be observed that an experiment having a total exposure period of 32 hours, for example, with determination of hourly growth increments, furnishes data for exposure periods of 1, 2, 3, etc., up to 32 hours, and the average hourly growth rate may be readily determined for any or all of these 32 different lengths of exposure period. The growth increment for any period of observation (time increment) is the difference between the measurement taken at the beginning and that taken at the end of that period of observation. The first measurement was always made at 10.00 a.m., 2 hours after the plants were placed in the plant chambers. For convenience in presentation, all growth increments are here stated in terms of hundredths of a millimeter.

As has been mentioned, the readings were made hourly in most cases, so that the time increments are usually single hours and the growth increments correspond to the same periods. With temperatures near the minimum and with those near the maximum for growth, however, hourly growth increments are so small as to render the probable error of measurement relatively great. In these cases, and in a few others, the period of observation was 3 hours. In a very few cases it was still longer.

Tests were made for nearly all temperatures from 12° to 43°, by differences of 1°C. For temperatures from 20° to 30° the total period of exposure was 12 hours; for other temperatures the total period was longer in many cases, ranging in length to 21 or even to 39 hours.

In the tables which follow, where the data for the individual plants are given, the cultures are numbered serially and the two plants of each culture are distinguished by the letters a and b. Thus plants 1a and 1b, 2a and 2b, etc., are pairs which were in the same culture, and hence in the same plant chamber at the same time. These detailed observations are given in order that the kind of fluctuations met with in the increment values may be placed on record.

Increments of growth for temperatures from 12° to 43°C. The great mass of individual growth increments need not be set forth here, but three representative groups of these data, to show the extent of their variation due to unknown causes and to illustrate their general character, are given in tables III, IV and V. Table III refers to low temperatures (12° to 15°), where growth is very slow; table IV refers to medium temperatures (30° to 34°), where growth is most rapid; and table V refers to high temperatures (40° to 43°), where growth is again very slow. The time increments, or periods of observation, have, generally, a length of a single hour for the medium temperatures, and one of 3 hours for the low and for the high temperatures, this difference being for reasons already given. The last column in each table gives the averages of the growth increments (for the corresponding time increments) for all the plants used.

It is at once to be noted, from tables III, IV and V, that the individual, unexplained variations which are apparent here are most pronounced with the low and with the high temperatures; as the limits for growth are approached the individual differences between the seedlings (their internal conditions) become more influential in conditioning the growth rate.

The average growth increments for the different observation periods, for temperatures from 12° to 43°, derived as in tables III, IV and V, are all brought together in table VI. The mean hourly rates are given in parenthesis, for all observation periods of more than 1 hour, and for periods of 1 hour the average increments themselves are mean hourly rates.

Aside from irregular variations in the hourly rates, it is obvious from table VI that, with increasing temperature, these rates increase from a first minimum (3, for the second 3-hour period at 12°) to a maximum (167, for the twenty-seventh hour at 31°) and then decrease to a minimum of zero (for the seventh 3-hour period at 41° and at 42°, and for the sixth 3-hour period at 43°). The magnitude of any mean hourly rate is seen to depend upon two conditions, (1) the temperature employed, and (2) the time period during which the plants have been previously subject to that temperature.

The last statement is the main general result of the present study and it does not appear to have been seriously considered heretofore, in the literature of the relation of plant growth to temperature. This generalization would have been more thoroughly established had the observations been continued longer with the temperatures below 31°, for there is no clear evidence, in the data at hand, that longer continued observation might not have discovered higher hourly rates than those recorded. For the temperatures above 31° the data are adequate to establish the point in question, however. The highest hourly rate (150) for 32° was obtained in the eleventh hour of the experiment; the highest (142) for 33° occurred in the fifteenth and nineteenth hours; the highest (144) for 34° occurred in the nineteenth hour; that (120) for 35° occurred in the seventh hour; that (104) for 36° occurred in the ninth

TABLE III

Increments of growth (hundredths of a millimeter), for shoots of maize seedlings, generally for time increments of 3 hours, at temperatures of 12° to 15°C., the latter maintained constant during the entire period of exposure, in each case. The individual plants, for each temperature, are numbered 1a, 1b, 2a, etc.

TEMPERATURE, C.	SERIAL NUMBER OF OBSERVATION	1a	1b	2a	2b	3a	3b	4a	4b	5a	5b	6a	6b	AVERAGE
12°	1 (3)[a]	50	25	25	75	50	50	.....	.....	.....	.....	.....	.....	46
	2 (3)	00	25	25	00	00	00	.....	.....	.....	.....	.....	.....	8
	3 (3)	25	25	00	25	50	50	.....	.....	.....	.....	.....	.....	29
	4 (3)	00	25	25	00	00	100	.....	.....	.....	.....	.....	.....	25
13°	1 (3)	25	50	25	50	50	50	.....	.....	.....	.....	.....	.....	42
	2 (3)	25	00	25	25	25	00	.....	.....	.....	.....	.....	.....	17
	3 (3)	25	25	25	25	25	25	.....	.....	.....	.....	.....	.....	25
	4 (3)	25	25	25	25	75	25	.....	.....	.....	.....	.....	.....	33
	5 (3)	50	50	25	50	50	50	.....	.....	.....	.....	.....	.....	46
	6 (8)	100	150	100	150	200	75	.....	.....	.....	.....	.....	.....	129
	7 (2)	25	25	75	.....	.....	25	.....	.....	.....	.....	.....	.....	38
	8 (3)	75	25	00	25[b]	50[b]	25	.....	.....	.....	.....	.....	.....	31
	9 (3)	75	50	25	75	75	25	.....	.....	.....	.....	.....	.....	54
	10 (4)	50	..	75	50	100	50	.....	.....	.....	.....	.....	.....	65
14°	1 (3)	50	50	50	50	50	100	.....	.....	.....	.....	.....	.....	58
	2 (3)	25	25	25	25	25	50	.....	.....	.....	.....	.....	.....	29
	3 (3)	50	75	50	.....	50	50	.....	.....	.....	.....	.....	.....	55
	4 (3)	50	50	50	75[c]	50	75	.....	.....	.....	.....	.....	.....	55
	5 (3)	75	75	50	50	50	75	.....	.....	.....	.....	.....	.....	63
	6 (8)	200	200	200	75	150	225	.....	.....	.....	.....	.....	.....	175
	7 (3)	50	75	100	75	75	75	.....	.....	.....	.....	.....	.....	75
	8 (3)	100	100	100	50	75	50	.....	.....	.....	.....	.....	.....	79
	9 (3)	25	75	.....	.....	100	100	.....	.....	.....	.....	.....	.....	75
	10 (3)	75	100	200[d]	75[d]	100	100	.....	.....	.....	.....	.....	.....	94
15°	1 (3)	50	50	50	75	150	125	25	50	50	50	25	50	63
	2 (3)	25	25	75	25	25	25	25	25	25	25	75	75	38
	3 (3)	50	100	75	100	75	75	75	50	50	100	25	50	69
	4 (3)	75	75	100	75	50	75	50	75	75	100	50	75	73
	5 (3)	75	75	75	100	75	75	100	100	100	100	75	100	88
	6 (1)	25	25	00	25	25	25	.....	.....	.....	.....	.....	.....	21
	7 (2)	...	...	.....	.....	.....	...	100[e]	75[e]	100[e]	100[e]	100[e]	50[e]	...
	8 (7)	...	...	.....	.....	.....	...	200	200	175	350	250	275	242
	9 (3)	...	...	.....	.....	.....	...	100	100	100	150	75	100	104
	10 (3)	...	...	.....	.....	.....	...	75	100	100	175	150	.....	120
	11 (3)	...	...	.....	.....	.....	...	100	100	125	125	75	175[f]	105

[a] The length of the observation period (in hours) follows its number, in parenthesis.
[b] For observation periods 7 and 8 combined, 5 hours, not included in average.
[c] For observation periods 3 and 4 combined, 6 hours, not included in average.
[d] For observation periods 10 and 11 combined, 6 hours, not included in average
[e] For observation periods 6 and 7 combined, 9 hours.
[f] For observation periods 10 and 11 combined, 6 hours, not included in the average.

TABLE IV

Increments of growth (hundredths of a millimeter) for shoots of maize seedlings, generally for time increments of one hour, at temperatures of 31° to 34°C., the temperature maintained constant, in each case, for the entire period of exposure. The individual plants, for each temperature, are numbered 1a, 1b, 2a, etc.

TEMPERATURE, C.	SERIAL NO. OF OBSERVATION PERIOD	1a	1b	2a	2b	3a	3b	4a	4b	5a	5b	6a	6b	AVERAGE
31°	1	25	50	125	50	50	25	.....	.....	.....	.....	.....	.....	54
	2	25	50	50	100	75	50	.....	.....	.....	.....	.....	.....	58
	3	75	100	100	75	125	100	.....	.....	.....	.....	.....	.....	96
	4	125	100	100	100	100	100	.....	.....	.....	.....	.....	.....	104
	5	150	100	100	175	150	125	.....	.....	.....	.....	.....	.....	133
	6	100	100	100	150	100	125	.....	.....	.....	.....	.....	.....	123
	7	150	100	100	150	125	125	.....	.....	.....	.....	.....	.....	125
	8	150	75	125	125	75	125	.....	.....	.....	.....	.....	.....	113
	9	100	125	125	150	125	125	.....	.....	.....	.....	.....	.....	125
	10	150	100	100	150	125	150	.....	.....	.....	.....	.....	.....	129
	11	150	100	100	150	100	100	.....	.....	.....	.....	.....	.....	117
	12	150	100	150	225	150	150	.....	.....	.....	.....	.....	.....	154
	13	125	100	75	200	100	175	.....	.....	.....	.....	.....	.....	129
	14	125	100	125	200	150	125	.....	.....	.....	.....	.....	.....	138
	15	150	150	125	150	100	150	.....	.....	.....	.....	.....	.....	138
	16	150	100	75	150	100	150	.....	.....	.....	.....	.....	.....	121
	17	150	125	125	150	75	150	.....	.....	.....	.....	.....	.....	129
	18	100	125	150	225	175	125	.....	.....	.....	.....	.....	.....	150
	19	150	150	125	150	150	125	.....	.....	.....	.....	.....	.....	142
	20	125	150	150	250	125	150	.....	.....	.....	.....	.....	.....	158
	21	125	100	150	200	100	150	.....	.....	.....	.....	.....	.....	138
	22	150	125	125	175	125	150	.....	.....	.....	.....	.....	.....	142
	23	125	150	150	175	125	125	.....	.....	.....	.....	.....	.....	142
	24	125	175	125	150	125	125	.....	.....	.....	.....	.....	.....	138
	25	150	150	100	150	175	125	.....	.....	.....	.....	.....	.....	142
	26	175	150	200	150	125	150	.....	.....	.....	.....	.....	.....	158
	27	175	150	175	225	150	125	.....	.....	.....	.....	.....	.....	167
	28	150	150	200	175	150	150	.....	.....	.....	.....	.....	.....	163
	29	150	125	200	175	125	175	.....	.....	.....	.....	.....	.....	158
	30	150	125	225	150	125	175	.....	.....	.....	.....	.....	.....	158
	31	150	125	150	150	125	175	.....	.....	.....	.....	.....	.....	146
	32	150	150	150	150	100	150	.....	.....	.....	.....	.....	.....	142
	33	150	125	175	175	125	125	.....	.....	.....	.....	.....	.....	146
	34	150	125	175	150	125	150	.....	.....	.....	.....	.....	.....	146
	35	150	175	150	175	125	150	.....	.....	.....	.....	.....	.....	154
	36	150	150	125	200	150	150	.....	.....	.....	.....	.....	.....	154
	37[a]	400	450	375	425	400	425[a]	.....	.....	.....	.....	.....	.....	413
32°	1	75	75	75	75	50	75	.....	.....	.....	.....	.....	.....	71
	2	75	75	75	75	75	75	.....	.....	.....	.....	.....	.....	75
	3	75	75	100	75	75	100	.....	.....	.....	.....	.....	.....	83

TABLE IV—Continued

TEMPERATURE, C.	SERIAL NO. OF OBSERVATION PERIOD	1a	1b	2a	2b	3a	3b	4a	4b	5a	5b	6a	6b	AVERAGE
32°	4	100	75	100	100	100	125	.....	.....	.....	.....	.....	.....	100
	5	125	100	100	100	75	125	.....	.....	.....	.....	.....	.....	104
	6	150	125	100	125	100	125	.....	.....	.....	.....	.....	.....	121
	7	100	100	100	125	100	150	.....	.....	.....	.....	.....	.....	113
	8	125	125	125	125	100	150	.....	.....	.....	.....	.....	.....	125
	9	125	125	125	100	100	150	.....	.....	.....	.....	.....	.....	121
	10	125	125	125	100	125	150	.....	.....	.....	.....	.....	.....	125
	11	125	150	150	125	175	175	.....	.....	.....	.....	.....	.....	150
	12	125	150	150	125	175	125	.....	.....	.....	.....	.....	.....	142
	13	125	150	125	150	125	150	.....	.....	.....	.....	.....	.....	138
	14	150	150	150	150	125	125	.....	.....	.....	.....	.....	.....	142
	15	125	150	150	100	150	125	.....	.....	.....	.....	.....	.....	133
	16	125	150	150	150	175	125	.....	.....	.....	.....	.....	.....	146
	17	125	125	150	150	175	150	.....	.....	.....	.....	.....	.....	146
	18	125	125	150	175	150	125	.....	.....	.....	.....	.....	.....	142
	19	125	125	125	150	150	125	.....	.....	.....	.....	.....	.....	133
	20	150	125	125	150	150	125	.....	.....	.....	.....	.....	.....	138
	21	125	150	125	175	125	150	.....	.....	.....	.....	.....	.....	142
	22[a]	450	400	450	450	425	425	.....	.....	.....	.....	.....	.....	433[a]
	23	450	450	425	425	400	425	.....	.....	.....	.....	.....	.....	429
	24	400	400	375	400	425	425	.....	.....	.....	.....	.....	.....	404
	25	400	400	425	400	450	425	.....	.....	.....	.....	.....	.....	417
	26	450	500	400	450	350	375	.....	.....	.....	.....	.....	.....	421
	27	400	400	250	325	275	375	.....	.....	.....	.....	.....	.....	338
33°	1	50	50	50	75	75	100	75	25	50	50	50	50	58
	2	75	75	100	75	75	50	75	50	50	50	50	25	63
	3	100	125	75	100	75	25	100	75	50	100	100	75	83
	4	100	75	75	75	125	75	100	75	75	100	100	75	88
	5	75	100	75	100	75	100	100	100	75	100	125	100	94
	6	100	100	100	125	125	150	100	100	100	125	125	100	113
	7	100	100	125	200	100	100	150	100	100	100	125	100	117
	8	125	100	75	100	100	125	125	125	100	125	125	100	110
	9	125	100	125	125	125	125	125	125	125	150	125	150	127
	10	100	125	100	150	125	100	125	100	100	125	150	125	119
	11	100	125	100	125	100	100	100	100	125	125	125	100	110
	12	125	125	100	150	150	100	125	125	150	150	125	125	129
	13	100	125	150	175	150	100	100	125	150	125	125	125	131
	14	100	100	125	175	175	100	125	100	150	125	125	150	129
	15	125	125	125	250	175	125	125	100	125	150	125	150	142
	16	125	125	100	150	175	100	125	125	125	125	125	150	129
	17	100	125	125	175	175	200	125	100	150	125	125	150	140
	18	100	125	75	75	150	50	150	100	125	150	125	100	110
	19	125	150	125	225	200	125	125	125	125	125	100	150	142
	20	100	100	125	125	150	125	200	125	125	125	125	150	131
	21	100	100	100	150	150	125	100	100	125	125	150	100	119

TABLE IV—Continued

TEMPERATURE, C.	SERIAL NO. OF OBSERVATION PERIOD	1a	1b	2a	2b	3a	3b	4a	4b	5a	5b	6a	6b	AVERAGE
34°	1	100	25	75	75	25	75	25	75	75	25	50	75	58
	2	100	25	50	25	50	50	50	125	75	50	50	25	48
	3	25	75	50	25	150	75	50	100	75	100	50	75	71
	4	50	100	100	50	100	75	50	100	100	100	75	100	83
	5	100	100	100	25	150	125	100	100	125	100	100	75	100
	6	125	125	100	50	100	100	75	100	125	125	75	100	100
	7	125	100	125	75	125	150	125	175	150	150	75	125	125
	8	100	100	100	75	125	100	75	175	150	125	100	125	113
	9	100	125	75	75	150	100	100	150	150	150	75	100	113
	10	150	175	150	100	125	125	75	175	125	100	100	100	125
	11	100	100	100	100	125	125	150	150	150	150	75	125	121
	12	100	150	100	75	100	125	25	175	125	125	100	100	108
	13	75	125	125	100	175	125	150	125	125	100	75	75	115
	14	100	125	75	75	125	125	25	150	150	125	75	100	104
	15	100	150	75	100	100	125	125	150	100	150	75	100	113
	16	150	150	100	125	200	150	75	175	125	175	75	100	133
	17	125	175	100	125	100	125	125	150	125	150	125	100	127
	18	125	125	50	100	150	100	100	125	150	125	75	75	108
	19	150	150	125	150	125	175	150	150	150	150	150	100	144
	20	175	150	150	125	175	125	100	125	100	175	75	75	129
	21	100	150	25	100	100	100	100	75	125	125	50	75	94

[a] Period 37 for 31° and periods 22 to 27 for 32° were 3 hours in length; note that the growth increments given, and the averages, are 3-hour rates.

hour; that (88) for 37° occurred in the seventeenth and nineteenth hours; that (84) for 38° occurred in the ninth hour; that (60) for 39° occurred in the third hour, etc. Obviously there is a tendency evident, for the highest hourly mean to be exhibited at an earlier hour with higher and higher temperature. At the same time, this highest mean is progressively lower with higher temperature.

From these results it is clear that, to define the temperature with which a given growth rate is to be expected, it is absolutely necessary to state the length of time during which the plants have been subjected to the action of the temperature in question.

Average hourly growth rates for various periods of exposure. Turning now to the question of determining the optimum temperature for prolonged growth, it follows directly from what has just been brought out that such an optimum cannot be defined without reference to the period of exposure, but, to make this conclusion more obvious and to bring the presentation of my data into conformity with other published work on this subject, the increments of growth, for each temperature, have been treated as though the

TABLE V

Increments of growth (hundredths of a millimeter) for shoots of maize seedlings, for time increments of three hours, at temperatures of 40° to 43°C.; the temperature maintained constant, in each case, for the entire period of exposure. The individual plants, for each temperature, are numbered 1a, 1b, 2a, etc.

TEMPERATURE, C.	SERIAL NO. OF OBSERVATION PERIOD	1a	1b	2a	2b	3a	3b	4a	4b	AVERAGE
40°	1	100	75	75	75	75	100	75	75	81
	2	125	150	125	175	125	125	100	100	128
	3	100	100	125	100	100	100	100	100	103
	4	50	100	50	25	50	100	75	75	66
	5	100	100	75	100	75	50	75	50	78
	6	75	75	75	50	50	50	50	75	63
	7	100	75	50	50	25	50	50	25	53
41°	1	75	50	50	50	50	75	.....	.....	58
	2	100	100	100	100	75	75	.....	.....	92
	3	75	50	50	75	50	50	.....	.....	58
	4	50	50	25	50	25	50	.....	.....	42
	5	50	25	25	50	25	25	.....	.....	33
	6	00	00	00	25	00	00	.....	.....	4
	7	00	00	00	00	00	00	.....	.....	0
42°	1	25	25	25	25	50	50	.....	.....	33
	2	50	50	50	50	25	50	.....	.....	46
	3	50	25	25	25	25	25	.....	.....	29
	4	50	25	25	25	00	25	.....	.....	25
	5	25	25	25	00	25	25	.....	.....	21
	6	25	00	00	25	25	00	.....	.....	13
	7	00	00	00	00	00	00	.....	.....	00
43°	1	25	50	50	50	25	25	.....	.....	38
	2	00	50	00	00	00	00	.....	.....	8
	3	25	00	25	25	00	25	.....	.....	17
	4	00	25	00	00	25	00	.....	.....	8
	5	25	00	00	00	00	00	.....	.....	4
	6	00	00	00	00	00	00	.....	.....	00
	7	00	00	00	00	00	00	.....	.....	00

period of exposure had been 3, 6, 9, etc., hours, and the average hourly rate for each plant, for each of these longer periods, has been determined. The results thus obtained for any given time period are those that would have been exhibited if the plants had not been measured excepting at the beginning and end of that period, as though the experiment had been discontinued after 3, 6, 9, etc., hours. Table VII presents samples of these detailed results, for temperatures of 12° to 14°, 20°, 21°, 31° to 34°, and 40° to 43°C. In the

TALBE VI

Average growth increments (hundredths of a millimeter) for shoots of maize seedlings, at constant temperatures of from 12° to 43°C., for consecutive observation periods; the temperature maintained constant throughout the entire period of exposure, in each case.

TEMPERATURE, C.	NO. OF PLANTS USED	SERIAL NO. OF OBSERVATION PERIOD	AVERAGE GROWTH INCREMENT
12°	6	1 (3)[a]	46 (15)[b]
	6	2 (3)	8 (3)
	6	3 (3)	29 (10)
	6	4 (3)	25 (8)
13°	6	1 (3)[a]	42 (14)[b]
	6	2 (3)	17 (6)
	6	3 (3)	25 (8)
	6	4 (3)	33 (11)
	6	5 (3)	46 (15)
	6	6 (8)	129 (18)
	6	7 (2)	38 (19)
	6	8 (3)	31 (10)
	6	9 (3)	54 (18)
	6	10 (4)	65 (16)
14°	6	1 (3)[a]	58 (20)[b]
	6	2 (3)	29 (10)
	6	3 (3)	55 (18)
	6	4 (3)	55 (18)
	6	5 (3)	63 (21)
	6	6 (8)	175 (22)
	6	7 (3)	75 (25)
	6	8 (3)	79 (26)
	6	9 (3)	75 (25)
	6	10 (3)	94 (31)
15°	12	1 (3)[a]	63 (21)[b]
	12	2 (3)	38 (13)
	12	3 (3)	69 (23)
	12	4 (3)	73 (24)
	12	5 (3)	88 (29)
	6	6 (1)	21
	6	7 (2)	88[c] (29)
	6	8 (7)	242 (35)
	6	9 (3)	104 (35)
	5	10 (3)	120 (40)
	6	11 (3)	105 (35)
18°	4	1 (3)	54 (18)
	4	2 (3)	81 (27)
18°	4	3 (3)	100 (33)
	4	4 (3)	106 (35)
20°	12	1	27
	12	2	31
	12	3	38
	12	4	40
	12	5	38
	12	6	46
	12	7	48
	12	8	48
	12	9	48
	12	10	60
	12	11	56
	12	12	58
	6	13	79
	6	14	50
	6	15	50
21°	4	1	25
	4	2	38
	4	3	50
	4	4	50
	4	5	50
	4	6	56
	4	7	56
	4	8	62
	4	9	50
	4	10	62
	4	11	69
	4	12	62
22°	4	1	31
	4	2	38
	4	3	44
	4	4	44
	4	5	38
	4	6	44
	4	7	63
	4	8	75
	4	9	88

[a] In all cases where the length of the observation period is other than one hour, its length (in hours) follows its serial number, in parenthesis.

[b] Growth increments for observation periods of more than one hour are followed by the calculated hourly rate, in parenthesis.

[c] For periods 6 and 7 together, a 3-hour period.

TABLE VI—Continued

TEMPERATURE, C.	NO. OF PLANTS USED	SERIAL NO. OF OBSERVATION PERIOD	AVERAGE GROWTH INCREMENT
22°	4	10	81
	4	11	88
	4	12	88
	4	13	81
23°	12	1	38
	12	2	48
	12	3	48
	12	4	63
	12	5	56
	12	6	60
	12	7	60
	12	8	85
	12	9	73
	12	10	81
	12	11	75
	12	12	83
24°	11	1	41
	11	2	52
	11	3	57
	11	4	61
	11	5	61
	11	6	77
	11	7	70
	11	8	79
	11	9	70
	11	10	82
	11	11	73
	11	12	100
25°	12	1	38
	12	2	65
	12	3	79
	12	4	71
	12	5	71
	12	6	77
	12	7	75
	12	8	75
	12	9	77
	12	10	81
	12	11	94
	12	12	102
26°	15	1	50
	15	2	67
	15	3	62
	15	4	75
	15	5	75
	15	6	95
	15	7	87
	15	8	88
	15	9	92
	15	10	105
	15	11	93
	15	12	90
27°	10	1	65
	10	2	73
	10	3	78
	10	4	85
	10	5	88
	10	6	85
	10	7	98
	10	8	95
	10	9	98
	10	10	108
	10	11	108
	10	12	110
28°	24	1	55
	24	2	76
	24	3	85
	24	4	92
	24	5	92
	24	6	94
	24	7	98
	24	8	111
	24	9	109
	24	10	127
	24	11	115
	24	12	127
29°	12	1	65
	12	2	75
	12	3	81
	12	4	83
	12	5	96
	12	6	88
	12	7	100
	12	8	96
	12	9	104
	12	10	119
	12	11	121
	12	12	125

TABLE VI—Continued

TEMPERATURE, C.	NO. OF PLANTS USED	SERIAL NO. OF OBSERVATION PERIOD	AVERAGE GROWTH INCREMENT
30°	9	1	81
	9	2	86
	9	3	100
	9	4	100
	9	5	97
	9	6	103
	9	7	117
	9	8	103
	9	9	108
	9	10	108
	9	11	144
	9	12	131
31°	6	1	54
	6	2	58
	6	3	96
	6	4	104
	6	5	133
	6	6	123
	6	7	125
	6	8	113
	6	9	125
	6	10	129
	6	11	117
	6	12	154
	6	13	129
	6	14	138
	6	15	138
	6	16	121
	6	17	129
	6	18	150
	6	19	142
	6	20	158
	6	21	138
	6	22	142
	6	23	142
	6	24	138
	6	25	142
	6	26	158
	6	27	167
	6	28	163
	6	29	158
	6	30	158
	6	31	146
31°	6	32	142
	6	33	146
	6	34	146
	6	35	154
	6	36	154
	6	37 (3)[a]	413 (138)[b]
32°	6	1	71
	6	2	75
	6	3	83
	6	4	100
	6	5	104
	6	6	121
	6	7	113
	6	8	125
	6	9	121
	6	10	125
	6	11	150
	6	12	142
	6	13	138
	6	14	142
	6	15	133
	6	16	146
	6	17	146
	6	18	142
	6	19	133
	6	20	138
	6	21	142
	6	22 (3)[a]	433 (144)[b]
	6	23 (3)	429 (143)
	6	24 (3)	404 (135)
	6	25 (3)	417 (139)
	6	26 (3)	421 (140)
	6	27 (3)	338 (113)
33°	12	1	58
	12	2	63
	12	3	83
	12	4	88
	12	5	94
	12	6	113
	12	7	117
	12	8	110
	12	9	127

[a] In all cases where the length of the observation period is other than one hour, its length (in hours) follows its serial number, in parenthesis.

[b] Growth increments for observation periods of more than one hour are followed by the calculated hourly rate, in parenthesis.

TABLE VI—Continued

TEMPERATURE, C.	NO. OF PLANTS USED	SERIAL NO. OF OBSERVATION PERIOD	AVERAGE GROWTH INCREMENT	TEMPERATURE, C.	NO. OF PLANTS USED	SERIAL NO. OF OBSERVATION PERIOD	AVERAGE GROWTH INCREMENT
33°	12	10	119	35°	10	13	95
	12	11	110		10	14	108
	12	12	129		10	15	110
	12	13	131		10	16	100
	12	14	129		10	17	105
	12	15	142		10	18	100
	12	16	129		10	19	85
	12	17	140		10	20	78
	12	18	110		10	21	95
	12	19	142				
	12	20	131		6	1	29
	12	21	119		6	2	54
					6	3	67
34°	12	1	58		6	4	63
	12	2	48		6	5	75
	12	3	71		6	6	88
	12	4	83		6	7	83
	12	5	100		6	8	92
	12	6	100		6	9	104
	12	7	125		4	10	100
	12	8	113		4	11	75
	12	9	113		4	12	75
	12	10	125	36°	4	13	75
	12	11	121		4	14	94
	12	12	108		4	15	119
	12	13	115		4	16	63
	12	14	104		4	17	75
	12	15	113		4	18	62
	12	16	133		4	19	69
	12	17	127		4	20	62
	12	18	108		6	21	50
	12	19	144		6	22 (3)[a]	188 (63)[b]
	12	20	129		6	23 (3)	154 (51)
	12	21	94		6	24 (4)	150 (38)
					6	25 (2)	8 (4)
35°	10	1	43				
	10	2	50		10	1	55
	10	3	78		10	2	48
	10	4	85		10	3	60
	10	5	93		10	4	78
	10	6	95		10	5	70
	10	7	120	37°	10	6	75
	10	8	83		10	7	60
	10	9	105		10	8	68
	10	10	85		9	9	72
	10	11	103		9	10	69
	10	12	90		10	11	73

TABLE VI—Continued

TEMPERATURE, C.	NO. OF PLANTS USED	SERIAL NO. OF OBSERVATION PERIOD	AVERAGE GROWTH INCREMENT
37°	10	12	60
	10	13	78
	10	14	70
	10	15	58
	4	16	94
	4	17	88
	4	18	56
	4	19	88
	4	20	69
	4	21	56
38°	8	1	25
	8	2	38
	8	3	31
	8	4	56
	8	5	63
	8	6	63
	8	7	75
	8	8	63
	8	9	84
	8	10	66
	8	11	59
	8	12	69
	8	13	56
	8	14	53
	8	15	59
	8	16	69
	8	17	47
	8	18	44
	4	19	56
	4	20	50
	8	21	50
	8	22	34
39°	12	1 (3)[a]	88 (29)[b]
	12	2 (3)	160 (53)
	12	3 (3)	181 (60)
39°	12	4 (3)	140 (47)
	12	5 (3)	127 (42)
	12	6 (3)	127 (42)
	12	7 (3)	100 (33)
40°	8	1 (3)[a]	81 (27)[b]
	8	2 (3)	128 (43)
	8	3 (3)	103 (34)
	8	4 (3)	66 (22)
	8	5 (3)	78 (29)
	8	6 (3)	63 (21)
	8	7 (3)	53 (18)
41°	6	1 (3)[a]	58 (19)[b]
	6	2 (3)	92 (31)
	6	3 (3)	58 (19)
	6	4 (3)	42 (14)
	6	5 (3)	33 (11)
	6	6 (3)	4 (1)
	6	7 (3)	0 (0)
42°	6	1 (3)[a]	33 (11)[b]
	6	2 (3)	46 (15)
	6	3 (3)	29 (10)
	6	4 (3)	25 (8)
	6	5 (3)	21 (7)
	6	6 (3)	13 (4)
	6	7 (3)	00 (0)
43°	6	1 (3)[a]	38 (13)[b]
	6	2 (3)	8 (3)
	6	3 (3)	17 (6)
	6	4 (3)	8 (3)
	6	5 (3)	4 (1)
	6	6 (3)	0 (0)
	6	7 (3)	0 (0)

[a] In all cases where the length of the observation period is other than one hour, its length (in hours) follows its serial number, in parenthesis.

[b] Growth increments for observation periods of more than one hour are followed by the calculated hourly rate, in parenthesis.

last column of this table are given the mean hourly rates of growth for all plants employed with each temperature.

Table VIII sets forth the means for all cases dealt with, including those from the last column of table VII.

TABLE VII

Hourly rates (hundredths of a millimeter) of growth of shoots of maize seedlings, for periods of 3, 6, 9, etc. hours, at temperatures of 12°–14°, 20°, 21°, 31°–34°, and 40°–43° C.; the temperature maintained constant during the entire period in each case.

TEMPERATURE, C.	LENGTH OF PERIOD	1a	1b	2a	2b	3a	3b	4a	4b	5a	5b	6a	6b	MEAN
	Hours													
12°	3	17	8	8	25	17	17	.....	.....	.....	.....	.....	.....	15
	6	8	8	8	13	8	8	.....	.....	.....	.....	.....	.....	9
	9	8	8	6	11	11	11	.....	.....	.....	.....	.....	.....	9
	12	6	8	6	8	8	17	.....	.....	.....	.....	.....	.....	9
13°	3	8	17	8	17	17	17	.....	.....	.....	.....	.....	.....	14
	6	8	8	8	13	13	8	.....	.....	.....	.....	.....	.....	10
	9	8	8	8	11	11	8	.....	.....	.....	.....	.....	.....	10
	12	8	8	8	10	15	8	.....	.....	.....	.....	.....	.....	10
	15	10	10	8	12	15	10	.....	.....	.....	.....	.....	.....	11
	23	11	13	10	14	18	10	.....	.....	.....	.....	.....	.....	13
	28	13	13	11	13	17	10	.....	.....	.....	.....	.....	.....	13
	31	14	13	10	14	18	10	.....	.....	.....	.....	.....	.....	13
	35	14	.....	11	14	19	10	.....	.....	.....	.....	.....	.....	14
14°	3	17	17	17	17	17	33	.....	.....	.....	.....	.....	.....	20
	6	13	13	13	13	13	25	.....	.....	.....	.....	.....	.....	15
	9	14	17	14	.....	14	22	.....	.....	.....	.....	.....	.....	16
	12	15	17	15	13	15	23	.....	.....	.....	.....	.....	.....	16
	15	17	18	15	13	15	23	.....	.....	.....	.....	.....	.....	17
	23	20	21	18	12	16	25	.....	.....	.....	.....	.....	.....	19
	27	19	20	19	13	17	24	.....	.....	.....	.....	.....	.....	19
	30	20	22	19	13	18	23	.....	.....	.....	.....	.....	.....	19
	33	19	22	.....	.....	19	24	.....	.....	.....	.....	.....	.....	21
	36	19	23	23	13	20	25	.....	.....	.....	.....	.....	.....	21
15°	3	17	17	17	25	50	42	8	17	17	17	8	17	21
	6	13	13	21	17	29	25	8	13	13	13	17	25	17
	9	14	19	22	22	28	25	14	14	14	19	14	19	19
	12	17	21	25	23	25	25	15	17	17	23	15	21	20
	15	18	22	25	25	25	25	18	20	20	25	17	23	22
	18	.....	.....	.....	.....	.....	.....	21	21	22	26	19	22	22
	25	.....	.....	.....	.....	.....	.....	23	23	23	33	24	27	26
	28	.....	.....	.....	.....	.....	.....	24	24	24	35	24	28	27
	31	.....	.....	.....	.....	.....	.....	24	25	25	37	27	.....	28
	34	.....	.....	.....	.....	.....	.....	25	26	26	38	26	28	28
20°	3	33	25	33	25	42	25	42	42	42	25	33	17	32
	6	42	33	42	29	37	25	42	42	46	33	33	33	36
	9	47	39	50	33	36	28	44	42	50	39	36	44	41
	12	52	44	54	38	39	31	48	46	54	44	42	50	45
	15	62	48	58	42	42	33	.....	.....	.....	.....	.....	.....	48

TABLE VII—Continued

TEMPERATURE, C.	LENGTH OF PERIOD	1a	1b	2a	2b	3a	3b	4a	4b	5a	5b	6a	6b	MEAN
	Hours													
21°	3	33	42	25	50	.....	.....	.....	.....	.....	.....	.....	.....	38
	6	42	46	42	50	.....	.....	.....	.....	.....	.....	.....	.....	45
	9	47	47	50	50	.....	.....	.....	.....	.....	.....	.....	.....	49
	12	54	54	52	50	.....	.....	.....	.....	.....	.....	.....	.....	53
31°	3	41	66	91	75	83	58	.....	.....	.....	.....	.....	.....	69
	6	83	83	96	108	100	87	.....	.....	.....	.....	.....	.....	93
	9	100	88	92	119	102	100	.....	.....	.....	.....	.....	.....	100
	12	112	91	106	133	108	108	.....	.....	.....	.....	.....	.....	109
	15	120	97	107	145	110	117	.....	.....	.....	.....	.....	.....	116
	18	119	100	108	148	111	120	.....	.....	.....	.....	.....	.....	117
	21	121	105	113	151	113	123	.....	.....	.....	.....	.....	.....	121
	24	123	110	115	153	114	125	.....	.....	.....	.....	.....	.....	123
	27	127	114	120	154	118	126	.....	.....	.....	.....	.....	.....	126
	30	130	116	128	156	120	130	.....	.....	.....	.....	.....	.....	130
	33	132	118	131	158	120	131	.....	.....	.....	.....	.....	.....	131
	36	133	121	133	158	121	133	.....	.....	.....	.....	.....	.....	133
	39	133	123	132	157	121	134	.....	.....	.....	.....	.....	.....	133
32°	3	75	75	83	75	66	75	.....	.....	.....	.....	.....	.....	72
	6	100	87	91	91	79	104	.....	.....	.....	.....	.....	.....	92
	9	106	97	100	100	86	119	.....	.....	.....	.....	.....	.....	101
	12	111	108	110	104	104	127	.....	.....	.....	.....	.....	.....	111
	15	115	117	116	110	110	128	.....	.....	.....	.....	.....	.....	116
	18	117	119	122	118	119	129	.....	.....	.....	.....	.....	.....	120
	21	119	121	123	124	122	129	.....	.....	.....	.....	.....	.....	123
	24	123	123	126	127	125	131	.....	.....	.....	.....	.....	.....	125
	27	126	126	128	128	126	132	.....	.....	.....	.....	.....	.....	127
	30	127	127	128	129	127	133	.....	.....	.....	.....	.....	.....	128
	33	127	127	129	129	129	134	.....	.....	.....	.....	.....	.....	129
	36	129	130	129	131	128	133	.....	.....	.....	.....	.....	.....	130
	39	132	130	125	129	125	132	.....	.....	.....	.....	.....	.....	128
33°	3	75	83	75	58	81	66	50	50	66	75	83	50	68
	6	83	87	91	83	91	91	71	75	83	79	91	71	83
	9	94	91	97	94	105	102	86	86	94	88	108	86	94
	12	98	100	104	96	108	110	91	96	108	92	116	94	101
	15	100	103	116	98	110	115	95	105	113	100	133	103	107
	18	101	107	125	101	114	116	97	109	116	100	134	108	110
	21	102	108	130	105	118	118	100	112	118	102	138	112	113
34°	3	41	41	58	41	75	66	41	100	75	58	50	58	59
	6	66	75	79	42	96	83	58	100	95	83	66	75	76
	9	80	86	86	52	108	94	72	122	114	102	72	88	89
	12	89	100	92	62	110	102	75	133	119	108	77	94	97

TABLE VII—Continued

TEMPERATURE, C.	LENGTH OF PERIOD	1a	1b	2a	2b	3a	3b	4a	4b	5a	5b	6a	6b	MEAN
	Hours													
34°	15	90	106	93	68	115	106	80	135	120	111	77	93	100
	18	97	114	91	76	120	109	83	137	122	118	79	93	103
	21	103	119	92	83	122	113	88	134	122	122	80	91	106
40°	3	33	25	25	25	25	33	25	25	....	....	....	....	27
	6	37	37	33	41	33	37	29	29	....	....	....	....	34
	9	33	36	36	39	33	36	31	30	....	....	....	....	34
	12	31	35	31	31	29	35	29	29	....	....	....	....	31
	15	31	35	30	31	28	32	28	26	....	....	....	....	30
	18	30	33	29	29	26	29	26	25	....	....	....	....	28
	21	30	32	27	27	23	27	25	24	....	....	....	....	26
41°	3	25	16	16	16	16	25	....	....	....	....	....	....	19
	6	29	25	25	25	21	25	....	....	....	....	....	....	25
	9	27	22	22	25	19	22	....	....	....	....	....	....	23
	12	25	20	19	23	16	20	....	....	....	....	....	....	20
	15	23	18	16	20	15	18	....	....	....	....	....	....	18
	18	19	15	12	13	12	15	....	....	....	....	....	....	14
	21	16[a]	13	10	11	10	13	....	....	....	....	....	....	12[a]
42°	3	8	8	8	8	8	16	....	....	....	....	....	....	9
	6	13	13	12	13	12	16	....	....	....	....	....	....	13
	9	14	11	11	11	11	14	....	....	....	....	....	....	12
	12	14	10	10	10	8	12	....	....	....	....	....	....	11
	15	13	10	10	8	8	12	....	....	....	....	....	....	10
	18	13	8	8	9	8	10	....	....	....	....	....	....	9
	21	11[a]	7	7	8	7	9	....	....	....	....	....	....	8[a]
43°	3	8	16	16	16	8	8	....	....	....	....	....	....	12
	6	4	16	16	8	4	4	....	....	....	....	....	....	9
	9	5	11	8	8	3	5	....	....	....	....	....	....	7
	12	4	10	6	6	4	4	....	....	....	....	....	....	6
	15	5	10	5	5	3	3	....	....	....	....	....	....	5
	18	4[a]	8	4	4	3	3	....	....	....	....	....	....	4[a]

[a] There was no growth at all during the last 3 hours, so that the hourly rates for the longest period here begin a regular decrease, which would continue indefinitely, assuming that growth does not again begin. In all these cases observations were continued through the 21-hour period.

An examination of the data given in tables VII and VIII brings out clearly enough the logical futility of any consideration of an optimum temperature for growth without at the same time considering the length of the exposure period.

With temperatures of from 12° to 15°, the mean hourly rate for the first 3 hours of exposure is much higher than it is for periods of 6 and 9 hours.

TABLE VIII

Mean average hourly growth rates (hundredths of a millimeter), for shoots of maize seedlings, at temperatures of from 12° to 43°, for observation periods of 3, 6, 9, etc., hours, the temperature maintained constant, in each case, throughout the entire period.

TEMP.	LENGTH OF EXPOSURE PERIOD, *hours*												
	3	6	9	12	15	18	21	24	27	30	33	36	39
deg. C.													
12	15	9	9	9	.....	.....	.....	.....	.....	.....	.....	.....	....
13	14	10	10	10	11	.....	.....	13 (23)[a]	13 (28)	13 (31)	.....	14 (35)	....
14	20	15	16	16	17	.....	.....	19 (23)	19	19	21	21	....
15	21	17	19	20	22	22	.....	26 (25)	27 (28)	28 (31)	28 (34)	.....	....
18	18	23	26	28	.....	.....	.....	.....	.....	.....	.....	.....	....
20	32	36	41	45	48	.....	.....	.....	.....	.....	.....	.....	....
21	37	44	48	53	.....	.....	.....	.....	.....	.....	.....	.....	....
22	37	39	51	59	.....	.....	.....	.....	.....	.....	.....	.....	....
23	44	52	59	64	.....	.....	.....	.....	.....	.....	.....	.....	....
24	50	58	64	69	.....	.....	.....	.....	.....	.....	.....	.....	....
25	60	66	70	75	.....	.....	.....	.....	.....	.....	.....	.....	....
26	58	65	75	82	.....	.....	.....	.....	.....	.....	.....	.....	....
27	70	78	83	90	.....	.....	.....	.....	.....	.....	.....	.....	....
28	72	80	89	98	.....	.....	.....	.....	.....	.....	.....	.....	....
29	88	89	94	105	.....	.....	.....	.....	.....	.....	.....	.....	....
30	77	94	100	108	.....	.....	.....	.....	.....	.....	.....	.....	....
31	69	93	100	109	116	117	121	123	126	130	131	133	133
32	72	92	101	111	116	120	123	125	127	128	129	**130**	128
33	68	83	94	101	107	110	113	.....	.....	.....	.....	.....	....
34	59	76	89	97	100	103	106	.....	.....	.....	.....	.....	....
35	56	74	84	86	89	92	92	.....	.....	.....	.....	.....	....
36	47	65	72	74	**76**	**76**	73	71	.....	.....	.....	.....	....
37	55	65	69	70	**72**	70	68	.....	.....	.....	.....	.....	....
38	31	46	55	**58**	57	56	53	47	.....	.....	.....	.....	....
39	31	41	**47**	46	46	45	43	.....	.....	.....	.....	.....	....
40	27	**34**	**34**	31	30	28	26	.....	.....	.....	.....	.....	....
41	19	**25**	23	20	18	14	(12)[b]	.....	.....	.....	.....	.....	....
42	9	**13**	12	11	10	9	(8)[b]	.....	.....	.....	.....	.....	....
43	**12**	9	7	6	5	(4)[b]	.....	.....	.....	.....	.....	.....	....

[a] Where the length of exposure period is not that given at the head of the column, the actual length is shown in parenthesis, after the corresponding rate.

[b] The last rate given for 41°, 42° and 43°, in parenthesis, is based on a period of exposure continuing 3 hours after all growth had ceased; it is, of course, a false average, in one sense.

These exceptionally high rates for the first 3 hours may be due to after-effects of the higher temperature to which the plants had been exposed previous to the beginning of the experiments. With longer periods, however, the high rate for the first 3 hours is equalled or surpassed, at least for temperatures of 13° to 15°. Whether periods still longer than 35 hours (for 13°), 36 hours (for 14°) or 34 hours (for 15°) might have given still higher mean hourly rates than the highest ones shown can, of course, not be stated.

Whatever may be the explanation of the high hourly means for the first 3 hours, it is clear that the means generally increase with longer periods, at least up to 34 to 36 hours.

For temperatures 20° to 30°, the mean hourly rates for each temperature also become generally of greater magnitude as the exposure period becomes longer. For temperatures 31° and 32°, where observation was longest continued, this statement still holds, but for 32° a maximum hourly mean (130) is encountered with a period of 36 hours, after which the magnitude of the mean apparently declines; the mean rate during the 39-hour period (128) is as low as that for the 30-hour period.

For temperatures 33° to 35°, as here given, the observations were discontinued too soon to show such a decrease in hourly rate as that just mentioned, if such decrease occurs. A special series at 33.5°, continued 36 hours (not represented in the tables), shows this, however; it gives the highest hourly rates (111 in each case) with exposure periods 30 and 33 hours long.

The decrease in question is clearly shown for temperatures 36° to 42°. For 35°, the 18 and 21-hour periods give the highest mean hourly rate (92), though the data do not show that a still longer period might not have exhibited a greater value. From 36° to 43°, however, the length of exposure period resulting in the highest mean rate becomes progressively shorter with higher temperature. These maximum means are indicated in table VIII by full-face type, and it is clearly seen that the positions of these numbers in the table picture a very regular curve.

It has been shown, then: (1) that in all cases, from 13° to 42°, the mean hourly rate of growth increases with periods of exposure of more than 3 hours; (2) that, with temperatures of 32°, 33.5°, and 36° to 42°, this increase reaches a maximum and is then followed by a decrease, as the periods become longer; and (3) that for temperatures above 31°, the maximum mean hourly rate is attained for shorter and shorter periods of exposure, as the temperature becomes higher. For 43°, it appears that a period of 3 hours gives a higher hourly rate than one of 6 or more hours; in other words, the maximum in question is attained within the 3-hour period, and is followed, as in the other cases, by a decrease.

DISCUSSION

The optimum temperature for growth. As has been emphasized, the term optimum temperature cannot be employed in the common, loose sense, as though there were a definite optimum for each plant. No definition of optimum temperature can be valuable unless it involves a consideration of time.

If we regard as the optimum "the highest temperature which can be permanently sustained without depression of function" (F. F. Blackman [05]), then it is clear that such an optimum cannot exist, for there is *no* tempera-

ture at which any given growth rate will be indefinitely maintained. Of course the optimum temperature for growth might be defined as the highest one which will allow growth *for some specified time period*, without decrease in rate, but here the condition of time is involved.

Again, if we consider, also with F. F. Blackman [05], that the optimum is that temperature for which "the retardation produced by exposure to superoptimal temperature must not be of the nature of permanent injury, and that therefore on cooling again to the optimum temperature there must be a return of the function to its highest value," it is obvious that the length of the period of exposure to "superoptimal temperature" must be specified. Otherwise there can be no such optimum.

It seems most useful to regard as the optimum that temperature which *for a specified period of exposure*, produces the greatest growth. On such a basis several optima are shown in table VIII.

Referring to that table, if the experiments had been made with a 3-hour period the optimum temperature deduced would have been 29°, with an average hourly rate of 88. If measurements had been made only at the beginning and end of the first 6 hours of exposure, the indicated optimum would have been at 30°, with an hourly growth rate of 94. The optimum temperature for 9 and for 12 hours of growth is clearly 32°. For longer periods the data at hand are not as clear, but it appears that a temperature of 32° is the optimum for 18 and 21, probably also for 24 and 27 hours, and that for longer periods (as far as shown) the optimum appears to shift to 31°. Whether the last observation is important cannot now be determined, but the consistency of the available data argues against this being due to uncontrolled conditions. Also, whether the optimum may shift over a range still somewhat greater than that from 29° (or below) to 32°, cannot be decided without longer continued series of observations. It seems to be clear, however that, *for periods of 3 hours or longer*, the temperature giving the greatest mean hourly rate of growth lies within the temperature range 29°–32°.

To bring out these relations in the usual manner growth curves have been constructed for the mean growth rates for periods of 3, 6, 9, 12, 15 and 21 hours as given in table VIII, and these curves are given in figures 2 and 3. They may be compared to the curve of figure 1, based on Koeppen's measurements for a period of 48 hours. In these curves the abscissae represent the temperature and the ordinates the mean hourly rate of growth, in hundredths of a millimeter.

It will be at once noted that there is not, in any of the curves of figures 2 and 3, any indication of such a double optimum temperature for growth, as is shown in Koeppen's curve. The most interesting feature of my curves lies in the shifting of the curve maximum already emphasized. Of course this shifting may be related to the same causes as those that produced Koeppen's double maximum, which, he ventured to suggest, might have been due to

"eine chemische Verbindung in einer solchen Weise, dass dadurch das Wachsthum eine Verzögerung erleidet." But, if such be the case, there is here no indication of it. Neither this suggestion nor that of MacDougal[21] in the same connection (to the effect that the first pronounced drop in Koeppen's curve might perhaps be due to phase changes of cell colloids and the second to the inhibition of specific enzyme action), requires *a priori* discussion here. I am of the opinion that the very pronounced irregularities in Koeppen's curve, the two greatest of which produce the apparent double optimum, are

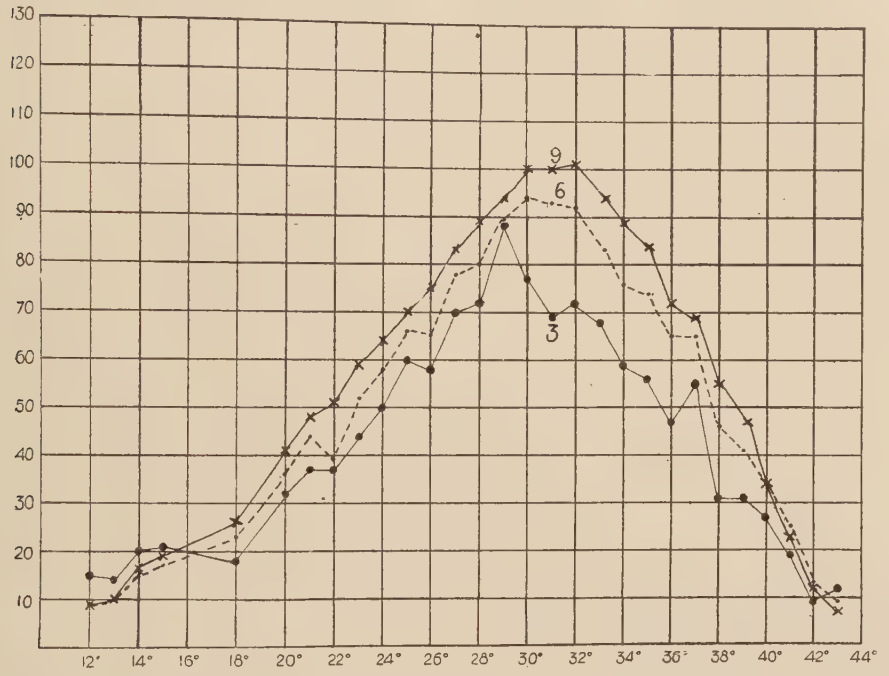

FIG. 2. Graphs showing the relation of temperature to average hourly growth rate, in shoots of maize seedlings, for 3, 6 and 9 hours, respectively. The variation in the optimum temperature, with different time periods, is shown. Ordinates are in terms of hundredths of a millimeter.

probably to be attributed to the small number of seedlings used by Koeppen, to features of his culture methods, and to his failure to select uniformly growing plantlets at the outset of each experiment. In short, these irregularities appear to have been due to unknown and uncontrolled conditions.

Aside from the irregularities of Koeppen's curve, my own agree with it in general form, excepting that the slopes on either side of the curve maximum are never nearly so steep as in Koeppen's. My curves for periods above 3 hours all agree in showing a rounded or flattened apex, in which

[21] MacDougal, D. T., The auxo-thermal integration of climatic complexes. Amer. Jour. Bot. 1: 186–93. 1914.

respect they also agree with the form that Koeppen's curve would assume if it were conventionalized in the usual way, suppressing the marked irregularities; the much discussed double optimum appears to be merely an indication of a rounded apex, denoting that a considerable temperature change in this region has but little effect upon the mean hourly rate of growth.

Relation of the growth rate to van't Hoff's law. The principle of chemical reaction velocity, to the effect that this velocity is doubled or trebled with each rise in temperature of 10°C., frequently termed the van't Hoff law,[22]

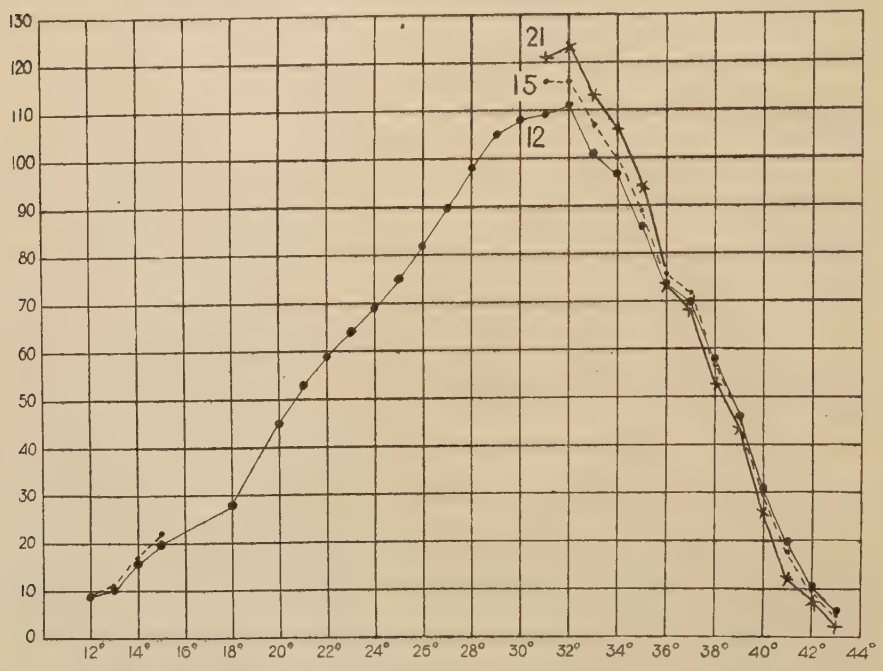

FIG. 3. Graphs showing the relation of temperature to average hourly growth rate, in shoots of maize seedlings, for 12, 15 and 21 hours, respectively. Ordinates are in terms of hundredths of a millimeter.

has been applied to physiological processes by numerous writers.[23] In dealing with this matter it is customary to employ the term *temperature coefficient* to denote the factor by which the process velocity in question is affected for each change in temperature of 10°C. This coefficient remains approximately constant within a certain range of temperature changes, beyond which its value alters markedly.

[22] Van't Hoff, J. H., Lectures on theoretical and physical chemistry, translated by R. A. Lehfeldt. London. No date (author's preface dated 1898). Part 1, page 227.

[23] A rather full list of references to this discussion are given in the following:—Livingston, B. E., and Livingston, G. J., Temperature coefficients in plant geography and climatology. Bot. Gaz. **56**: 349–75. 1913.

For the process of respiration in lupine seedlings and Syringa flowers, Clausen [90] found the temperature coefficient to have a value of 2.5 for a range from 0° to 20°C. Matthaei [04] showed that the rate of photosynthesis in leaves of cherry-laurel is affected by a temperature coefficient of 2.1, for a range from 9° to 19°C. For sunflower leaves she found the corresponding coefficient to be 2.3. Balls[24] showed the van't Hoff law to hold for the process of growth in the "sore-shin" fungus, and Herzog[25] found the same to be true for spore-formation in *Saccharomyces pasteurianus*. Price [11] concluded that, "on the whole, an increase in temperature of 10°C. for a given kind of bud [of deciduous fruit trees] lessens the time of blooming by about one-half" (page 210). The same author shows a photograph of maize seedlings grown one week at 21°, 26° and 31°C., respectively, which appears to

TABLE IX

Temperature coefficients for growth rate of shoots of maize seedlings, for various 10° ranges of temperature, the time period being 12 hours.

TEMPERATURE RANGE	RANGE OF GROWTH RATE	COEFFICIENT
deg. C.	*0.01 mm.*	
12–22	9– 59	6.56
13–23	10– 64	6.40
15–25	20– 75	3.75
18–28	28– 98	3.50
20–30	45–108	2.40
21–31	53–109	2.06
22–32	59–111	1.88
25–35	75– 86	1.15
32–42	111– 11	0.09
33–43	101– 6	0.06

exhibit a coefficient of nearly 4 for this temperature increase of 10°, but he fails to refer to this matter in the text. In general, it appears that many or most physiological processes follow the van't Hoff principle within a medium range of temperatures, having temperature coefficients of from about 2 to about 2.5.

The growth measurements of the present study furnish data for determining within what limits this process, in shoots of maize seedlings, may follow the chemical principle. Considering only the mean hourly growth rates for a period of 12 hours, table IX gives the temperature coefficients effective for various 10° variations in temperature.

[24] Balls, W. L., Temperature and growth. Ann. Bot. **22**: 557–91. 1908.
[25] Herzog, R., Zur Biologie der Hefe. Zeitschr. physiol. Chem. **37**: 396–9. 1903.

Of course the coefficients of table IX would necessarily alter to some extent in their relations if any other time period than 12 hours were taken as basis for the growth rates. The table shows that the coefficient varies from 2.40 to 1.88 with the temperature range 20° to 32°. The latter range is but a small portion of the total temperature range within which growth of maize seedlings is shown to occur, but it is interesting to note that 20° to 32° represents the order of the temperature range usually experienced in maize-growing regions during the days when the plantlets are at a stage of growth comparable to that with which this study deals.

As in the case of most chemical reactions, the magnitude of the coefficient decreases as the temperature increases; and, conversely, this magnitude is simply approximately constant for a limited range of medium temperatures.

On the whole, the van't Hoff principle appears to apply to the growth process in maize seedlings and variation in the temperature coefficient is confined to a range of about 1.88 to 2.40, for the temperature range 20° to 32°C.

Minimum temperature for growth. The data here set forth show that the minimum and the maximum, like the optimum, temperature for growth must be considered as conditioned by the length of the period of exposure as well as by the temperature itself.

The minimum must needs be defined as the temperature at which growth ceases *after a specified exposure period.* The lowest temperature here dealt with (12°) is clearly still well above the minimum for an exposure period of 12 hours or less; growth, although slow and irregular, was not apparently brought to a standstill during the 12-hour experiments at 12°.

As to whether the hourly growth rate at low temperatures falls or rises, or remains constant, with increasing length of exposure period, this matter has attracted attention in the literature and may be given brief consideration here. Kirchner[26] found that low temperatures retarded plant growth often a longer or shorter period of time. He observed "ein allmähliches Sinken der Zuwachse innerhalb gleicher Zeiträume, welches in manchen Fällen erst nach einigen Wochen, in andern schon nach einem bis wenigen Tagen mit völligen Wachsthums-Stillstande, resp. mit dem Turgorverlust der Wurzel endigt."

Askenasy [90] obtained very different results from a similar inquiry, concluding that there is no such decrease in growth rate as Kirchner found. He suggests that this disagreement is due to improper treatment of Kirchner's seedlings. Askenasy finds, in his own results, "durchaus keinen Anhalt dafür, dass bei niederer Temperatur ein constantes Fallen der Zuwachsgrössen statt findet . . . . ."

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[26] Kirchner, O., Ueber das Längenwachsthum von Pflanzenorganen bei niederen Temperaturen. Biol. Pflanzen 3: 335–64. 1883.

In my own experiments (table VI) there occurred a fall in growth rate after the first three hours at 12° to 15°C., but this fall was followed (with temperatures of 13° to 15°) by a gradual increase in the hourly rate, this increase being continued up to 35 hours, in the case of 14°, and at least to 31 hours, in that of 15°. As has been remarked, it is very difficult to work precisely at these low temperatures, on account of the low growth rates here encountered.

Maximum temperature for growth. If the maximum temperature is defined similarly to the minimum and optimum, in terms of Centigrade degrees and time of exposure, we find (table V) that a temperature of 40° still allowed growth in all the plants tested, at least for a period of 21 hours; therefore, 40° is not the maximum for time periods below 21 hours. The three still higher temperatures tested all produced cessation of growth within the period of the experiments. With a temperature of 41° all but one of 6 plants exhibited no growth after 15 hours, the remaining plant ceased to grow after 18 hours. With 42°, 3 plants ceased growth after 15 hours and 3 after 18 hours. With 43° 3 plants grew no more after 9 hours, 2 ceased to grow after 12 hours, and growth of the remaining plant was stopped after 15 hours. Finally, it may be stated that 43°C. is the maximum temperature for growth of these seedlings, for an exposure period of 15 hours; 42° is the corresponding maximum for 18 hours. For time periods shorter than 15 hours the maximum temperature was not attained in the present series, but it must obviously be higher than 43°C.

Plants kept at these high temperatures (41° to 43°) for 6 hours after growth had ceased were not killed; when the temperature was gradually lowered growth was resumed.

Alteration in mean hourly growth rate with prolonged exposure to constant temperature. It appears from the data of table VI that, for all temperatures from 13° to 42°, the actual growth rate becomes greater as time goes on. With temperatures above 30° this increased actual rate is shown to reach a maximum and then to decline, but there is considerable apparent irregularity in the time required, with the various temperatures, for the attainment of the maximum average rate of growth.

This alteration in growth rate for successive hours of the prolonged exposure period is evidenced in the similar but much more regular march of the mean hourly rates derived from longer and longer periods, as brought together in table VIII. As has been pointed out, the length of period required to give the maximum mean hourly rate of growth for a given temperature, at least from 31° upward, becomes shorter with higher temperature. Thus for 31° this mean increases with longer and longer periods, up to 36 hours, and no decrease is noted with a period of 39 hours. With 32° this value increases until the period of exposure attains a length of 36 hours, and after 39 hours a decrease is evident. This decrease is shown with a period of only 6 hours

at a temperature of 43° and the points in table VIII, at which the maximum values of the mean hourly rates occur, for the temperatures from 32° to 43°, clearly arrange themselves in a very regular curve.

The general phenomenon of decreased rate with prolonged exposure to high temperature has been pointed out and discussed by a number of writers, with reference to growth as well as other processes. Thus, Sachs [75], as early as 1863, showed that Mimosa can withstand a temperature of 50°C., or even higher, for several minutes, but too long exposure produced death.

Eidam,[27] subjected Bacterium termo to a temperature of 45° to 47°C., for from 30 minutes to 3 hours, and found that this produced no ill effects; when subjected, however, to such temperature for a period longer than 4 hours, its growth subsequently, at a lower temperature, was retarded.

Ward,[28] studying cell division and growth of Bacillus ramosus in relation to temperature, says (page 446), "With high temperature cultures I never got anything like so large a crop at 30–35°C. as at 22–25°C., other things being equal. Moreover, it seems clear that though the growth may, for a short time, be as rapid as it is near the optimum, it soon slows down."

Ewart,[29] in his studies of the relation of temperature to the rate of protoplasmic streaming, found that at 30°C. a decrease in rate was manifested after a period of 20 minutes; at 45°C. there was a marked decrease of rate after but 6 minutes.

Turning our attention to more definitely chemical processes, in fermentation, according to Chudiakow [94], a decrease in rate is manifested at 25°C. after 5 hours; a more rapid decrease is shown at 35°C., in 2 hours; at 40°C. the decreased rate manifests itself from the beginning of the exposure to this temperature.

In a study of photosynthesis in relation to light, Pantanelli[30] found that with the higher light intensities a decrease in the photsynthetic values occurs after a period of time.

My own results are in general conformity with Matthaei's [04] first and third laws of the temperature control of photosynthesis at high temperatures. That writer's second law (namely, "the higher the temperature the more rapid is the rate of falling off"—see also F. F. Blackman [05], page 283) is not always so clearly shown here.

F. F. Blackman [05] has called attention to the significance of the decrease in the velocity of physiological processes occurring with prolonged exposure to high temperatures, and he has well emphasized the importance of this

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[27] Eidam, E., Die Einwirkung verschiedener Temperaturen und des Eintrocknens auf die Entwicklung von Bacterium termo (Duj.). Biol. Pflanzen **1**: 208–24. 1875.

[28] Ward, H. M., On the Biology of Bacillus ramosus (Fraenkel) a Schizomycete of the River Thames. Proc. Roy. Soc. Lond. **58**: 265–468. 1895.

[29] Ewart, A. J., On the physics and physiology of protoplasmic streaming in plants. Oxford, 1903.

[30] Pantanelli, E., Abhängigkeit der Sauerstoffausscheidung belichteter Pflanzen von äusseren Bedingungen. Jahrb. wiss. Bot. **39**: 167–228. 1904.

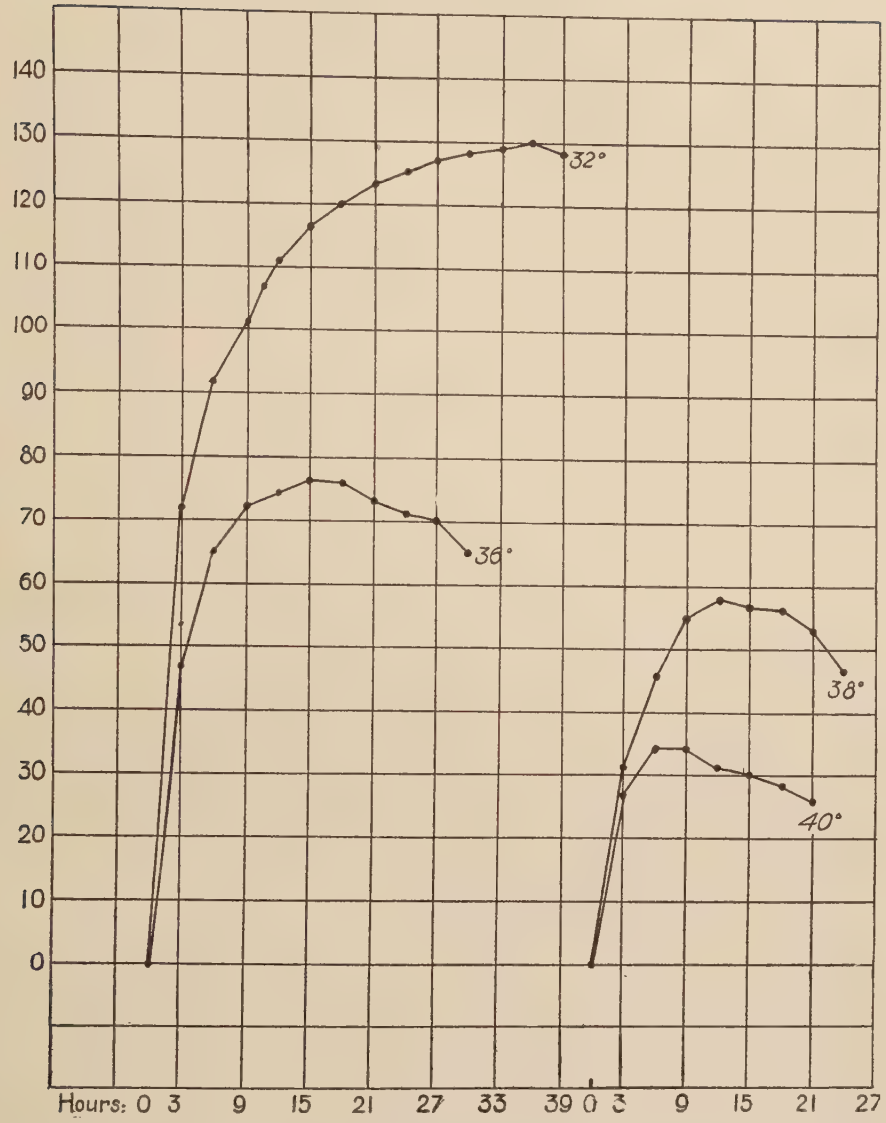

FIG. 4. Graphs showing the average hourly growth rates, in shoots of maize seedlings, for periods of 3, 6, 9, etc. hours, with maintained temperatures of 32°, 36°, 38° and 40°C. Ordinates are in terms of hundredths of a millimeter.

decrease in the determination of the position of the optimum temperature. From Matthaei's data Blackman points out that, in order to detect the maximum rate of photosynthesis, the initial measurement, especially with high temperatures, must be obtained as soon as possible after the beginning of the exposure period. My own data exhibit the decrease in hourly rate

of growth as beginning after a much longer period than is the case with photosynthesis, so that, to detect the maximum rate it appears unnecessary to begin observation until after nearly 3 hours with 43° temperature, and a longer time period may safely elapse in the case of lower temperatures. The initial time period should not be longer than 39 hours for 31°.

The march of the mean hourly growth rate for maize seedlings, with increasing length of exposure period, is shown graphically in figure 4, for the temperatures 32°, 36°, 38° and 40°C. The data are taken from table VIII. The initial rise in this mean rate is very rapid but the curves become less steep as the curve maximum is approached. This kind of phenomenon also occurs with growth of *Bacillus ramosus*, according to Ward [95], who says (page 446), "at the optimum it metabolises, and grows and respires, etc., at its best; but at higher temperatures removed from that it may grow for a short time more rapidly, but soon exhausts itself, and so produces a poorer crop in the end." Also, the effects of high temperature on the velocity of enzyme action, as obtained by Tammann[31] and others, agree most beautifully with the results on growth herein recorded. In this general connection it may be mentioned that the effects of high temperatures upon certain animal processes—such phenomena as heat-depression,[32] for example—show some interesting analogies to the matters here considered.

An explanation of the regular alteration in growth rate, occurring with sufficiently prolonged exposure to high temperatures, cannot yet be even attempted in any useful way, even in the realm of pure theory. Growth is such an exceedingly complex process that the interpretation here needed must await much more complete analysis of growth relations in general than has yet been possible. Some of the external conditions of growth are fairly easy to control and our knowledge of these as limiting factors is already considerable, but of internal conditions, within the plant, we know practically nothing of a quantitative nature.

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[31] Tammann, G., Zur Wirkung ungeförmter Fermente. Zeitschr. physik. Chem. **18**: 426–42. 1895. See also Herzog [03].

[32] Winterstein, H., Ueber die Wirkung der Wärme auf den Biotonus der Nervencentren. Zeitschr. Allg. Physiol. **1**: 129–41. 1902.

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VITA

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